BULLETIN

OF

ENTOMOLOGICAL RESEARCH.

ISSUED BY THE COMMONWEALTH
INSTITUTE OF ENTOMOLOGY

EDITOR: THE DIRECTOR

VOL. 49.

LONDON:

COMMONWEALTH INSTITUTE OF ENTOMOLOGY,
56, QUEEN'S GATE, S.W.7.

1959. ?

Head Office—c/o British Museum (Natural History), Cromwell Road, London, S.W.7.

Publication Office and Library—56, Queen's Gate, London, S.W.7.

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DATES OF PUBLICATION IN PARTS

Part I pp. 1–200	..	20 March 1958
Part II pp. 201–414	..	1 July 1958
Part III pp. 415–630	..	30 September 1958
Part IV pp. 631–802	..	4 December 1958

ERRATA

Page 77, fig. 1
Page 114, Table I, col. 2, 1 line from end
Page 120, line 17
} for " Geesecroft " read " Geescroft "

Page 135, line 20, for " *Filcalbia* " read " *Ficalbia* "
Page 557, line 1, for " with " read " was "
Page 582, 15 lines from end, after " then, when " insert " the population was expressed as the number of palms searched per nymph found and "

COMMONWEALTH INSTITUTE OF ENTOMOLOGY.

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OF
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Vol. 49. 1958.

THE BIOLOGY OF THE SUDAN BOLLWORM, *DIPAROPSIS WATERSI* (ROTHS.), IN THE GASH DELTA, SUDAN.

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Fison's Pest Control Ltd., Cambridge.

In 1951, the Gash Board, Aroma, in collaboration with the Research Division of the Ministry of Agriculture, Sudan, and by contract with Pest Control (Sudan) Ltd., appointed a research team to study the insect pests of cotton in the region of the Sudan known as the Gash Delta. The investigation had particular reference to the status, biology and control of the Sudan bollworm (*Diparopsis watersi* (Roths.)), the spiny bollworms (*Earias* spp.), the so-called American bollworm (*Heliothis armigera* (Hb.)) and the pink bollworm (*Platyedra gossypiella* (Saund.)), and was carried out under the direction of the Government Entomologist of the Sudan.

The present paper is concerned with certain aspects of the biology of the Sudan bollworm, which were studied over the period 1951–1955.

Climate.

The Gash Delta lies between approximately 15°30′ and 16°30′N. lat., in the Kassala Province of the eastern Sudan. Rainfall is seldom very heavy, averaging 187 mm. (approx. 7·5 in.) per annum at Aroma, in the middle of the delta. Although variable, it tends to decrease from south to north within the delta. Most of it falls in July–September, but light showers of little importance may occur during April–June and October–November in some years. Air temperatures (fig. 1) are high throughout the year, with highest daily maxima in April–June, and lowest daily minima in December–January. A drop in daily maxima normally occurs during August. Relative humidity (fig. 2) is highest during the rains and lowest in March–May. Heavy dews may occur in December–January. From April to October the prevailing wind is from the south, and over the remainder

* Seconded to the Research Division, Ministry of Agriculture, Sudan Government, for the period over which this investigation was made.

of the season from the north. The change from south to north in wind direction heralds the onset of cooler weather. From March to the beginning of the rains in July, heavy dust storms are frequent.

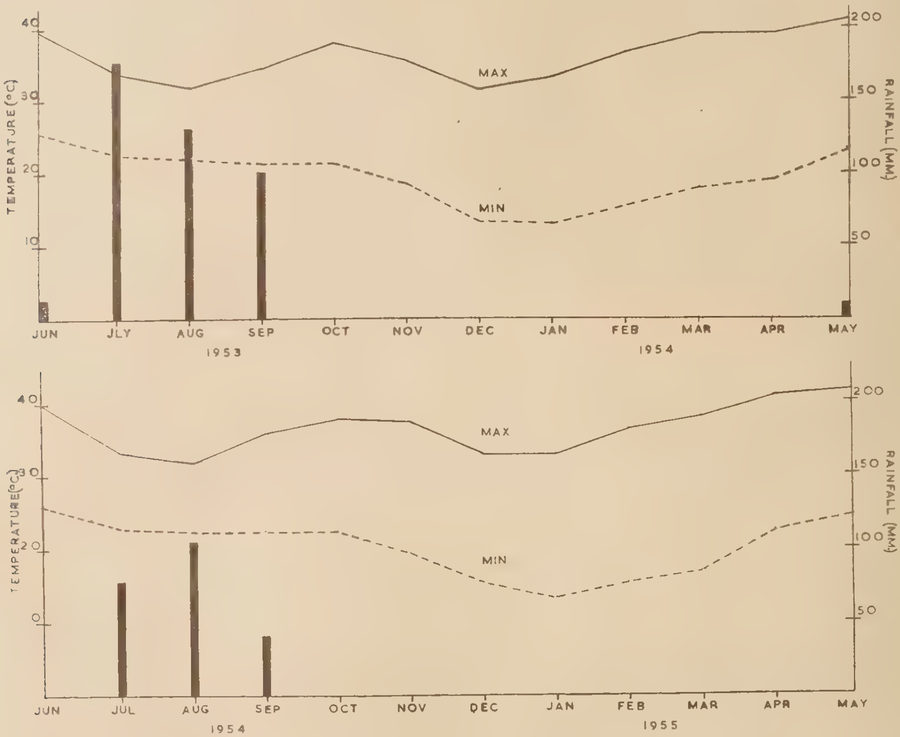

Fig. 1.—Mean daily maximum and minimum air temperatures and total monthly rainfall. Aroma, 1953/54 and 1954/55 seasons.

Method of cultivating Cotton.

Tothill (1948) and Richards (1950) have described the method of cotton cultivation in detail. The delta (fig. 3) consists mainly of an alluvial soil deposited by the River Gash, which rises in the Eritrean mountains south of Asmara. The river has an annual flood, which reaches the delta towards the end of June or the beginning of July and continues until October. It is only during the months of July, August and September that irrigation of the land is possible. Rainfall has little direct effect on the cotton crop, although it may encourage weed growth, especially on later flooded land. The heavy dews during the winter months may have a beneficial effect on plant growth.

Irrigation is of the controlled-flush type, which consists essentially of leading water to a point from which it may flow over suitably prepared land. Canals, from off-takes spaced at intervals along the course of the river, lead the water to suitable areas of cultivable land, bounded usually, for the purpose of irrigation, by earthen banks. These areas vary in size from 100 to 7,000 feddans * and are of irregular shape, although their length, which may be some five to ten miles, is considerably greater than their width (fig. 3). Irrigation commences in July and continues for as long as the level of the water is maintained in the river,

* 1 feddan = 1·038 acres = 0·420 hectares.

which is usually until the end of September. The amount of water entering a canal or area is controlled by mechanical regulators, but the flow of water over the land itself can be controlled only by the erection of earthen banks. The water has a very high silt content, which ranged from 3,323 to 5,769 parts per million at the head of the delta in 1939, and the occurrence of heavy silt deposits, especially at the mouth of the cultivated areas, may change considerably the course of the water over a field on successive waterings. Fortunately, the slope of the land is

Fig. 2.—Mean daily relative humidity (mean of 8 a.m. and 2 p.m. readings). Aroma, 1953/54 and 1954/55 seasons.

generally sufficiently steep to prevent silting-up of the canals. Owing to the method of irrigation, watering is heaviest at the mouths of the fields, there being a general decrease in the period of watering along the length of any area. It has been the practice to utilise the more lightly watered areas for the cultivation of sorghum.

The irrigated area situated at the head of the delta and known as Wad Sherifai is watered on a different basis, being divided into a number of small areas or "hods" which are flooded individually from the river. This system of irrigation results in a more even watering but leads to serious silting problems.

Along each canal the fields are divided into two blocks, the first and second "rotations", so that maximum advantage can be taken of the capacities of the respective canals. The first-rotation fields on each canal are opened during July and receive water for a period of 20–50 days, depending upon the length of the field, availability of water, and soil type. Following the closing of these fields during August, the second-rotation land is opened and receives a similar amount of water or, in a year of poor flood, as much water as is available before the flow finally ceases. Thus, there is an interval of approximately one month between the closing of the first- and second-rotation fields.

In addition, there are extensive areas of land, termed "balag", which are watered by natural overflow of the river. They vary greatly in extent, and are often under water from July to October. Cultivation of cotton on the balag areas is a post-war development which has led to the extension of the growing and picking seasons and curtailment of the "dead" season for cotton.

The total effective area of land watered for cotton and the relative proportion of first to second rotation vary considerably from season to season, and are wholly dependent upon the magnitude and duration of flow of the River Gash. In 1951, the total effective area watered was no more than 35,000 feddans, while in 1952, a year in which the flood was excellent, the area was as much as 70,000 feddans. It will be seen (fig. 4) that since 1946–47 there has been a marked tendency to

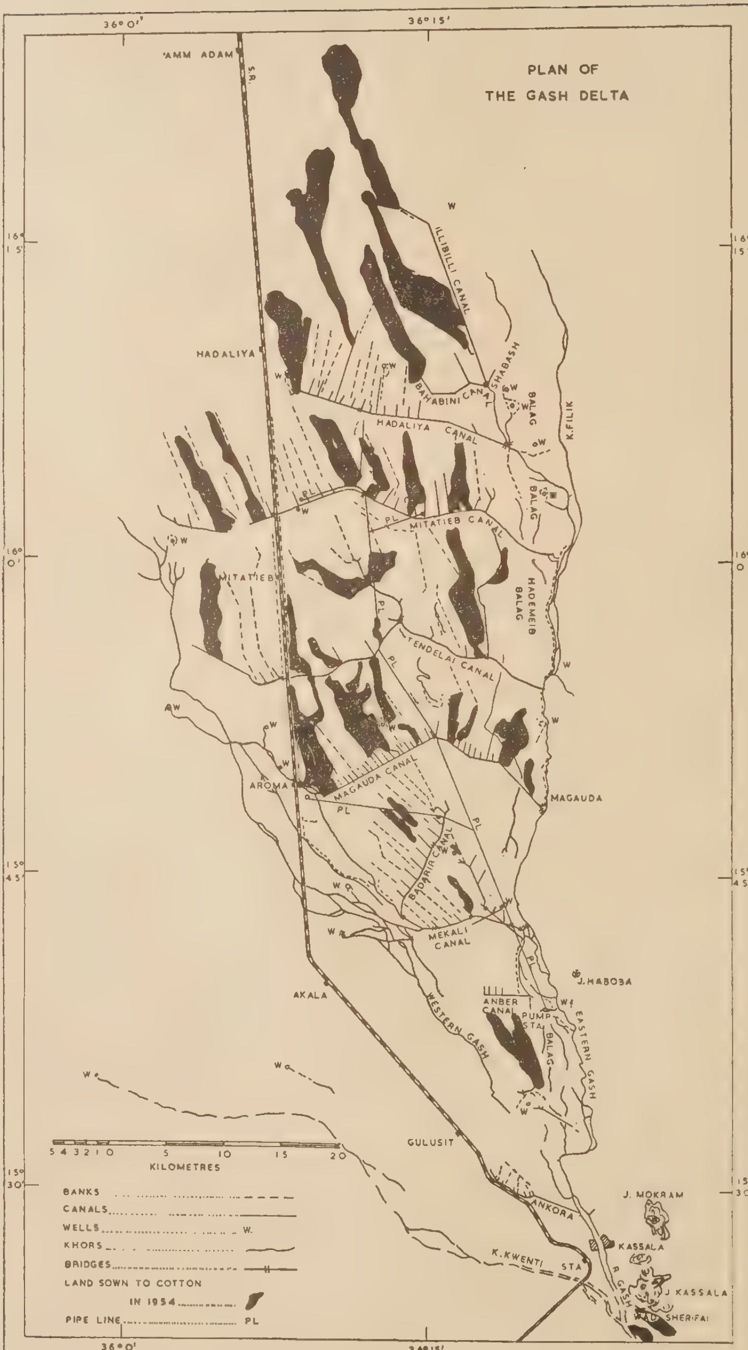

Fig. 3.—Plan of the Gash Delta showing areas of land sown to cotton in 1954.

increase the area of land under cotton. This has come about through the use of heavy earth-moving equipment, resulting in improved methods of water-control and the opening of fields as soon as the first spates occur. Formerly, land was opened only after the River Gash had been flowing for some time and showed promise of maintaining a steady level.

Fig. 4.—Effective area of land under X1730A and Domains Sakel cotton in the Gash Delta, 1937 to 1955.

Prior to 1953, cotton was grown on a four-year cycle, namely, cotton followed by three years of resting, but, in an attempt to control *Diparopsis* by flooding, this has now been altered to two years cotton followed by a rest period of two or three years. On Wad Sherifai and the balags, the rest period is omitted and cotton is sown every year. Egyptian-type cottons are grown, the two main varieties since 1937 being X1730A and Domains Sakel. American Upland cotton,

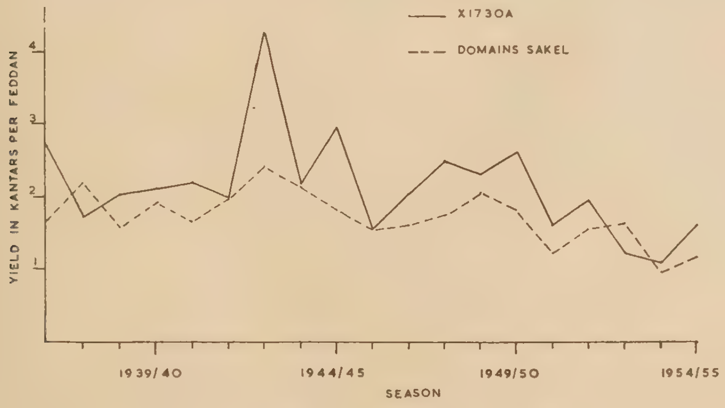

Fig. 5.—Yields of seed cotton for the two varieties, X1730A and Domains Sakel, in the Gash Delta, 1937 to 1955.

namely Wilds Sus. 16/1, has been grown on an experimental scale only. The susceptibility of Sakel to leaf-curl disease prevents this variety being sown before the middle of September, and thus the practice is to sow all first-rotation land with X1730A, and to reserve that of the second rotation for Sakel. In this way, X1730A cotton is sown approximately one month earlier than Sakel.

Before flooding, the land is cleared of the bush that has grown up over the period of rest and, as a rule, receives no further attention until after the cotton is sown, although over the past few years an attempt has been made to disc-plough as much of the land as possible to a depth of 8–12 in., in order to combat the growth of the sedge, *Cyperus rotundus*. The ploughing also has a favourable effect on the subsequent water-retaining capacity of the soil. Cotton seed is sown approximately one week after the cessation of flooding. Although the growth of weeds during and after flooding may make it desirable, on some areas, to hoe the land before sowing, many cultivators will sow the cotton amongst the heavy weed growth, in which case plant progress is retarded. Sowing is carried out with a planting stick or "seluka". The seed rate is almost invariably too high, upwards of twenty seeds per plant hole being no exception. Spacing between plant holes varies greatly, averaging 1·5 metres either way, and little attempt is made to sow in straight rows.

Plant populations are very low and average 5,000 plants per feddan. This figure includes plants of all sizes, so that the effective population must be considerably less. When the plants have reached a height of about six inches, the crop is hoed. A second, and in some cases, a third hoeing may follow if weed growth is excessive. After the final hoeing, which is completed during November, the land receives no further cultivations. Thinning of the plants to five per hole should be carried out when the plants are 1–2 ft. high, but this operation is done rather haphazardly by the cultivators, and at any time during the season it is possible to find holes containing ten or more plants.

Cotton picking begins in January on first-rotation cotton and somewhat later on second-rotation, and is continuous to the end of the season. Yields of seed cotton are low (fig. 5), and over the period 1951–55 averaged 1·40 and 1·37 kantars * per feddan for X1730A and Domains Sakel, respectively. The season ends officially on 30th April, after which the cotton stalks are pulled and burnt. This ensures a dead season of at least two months, the balag areas excepted. In some seasons, however, the presence of late-growth cotton, a common feature in the Gash Delta, may result in picking continuing into June, thereby restricting the dead season to a few weeks. Prior to 1954, only Sakel cotton was pulled, X1730A being cut at ground level. Cutting did not result in the death of the plants and ratoon growth occurred during the rains, which often necessitated a second cutting-out in October.

The method of cotton cultivation in the Gash Delta is still to a large extent primitive and results in a very uneven crop. The plants may grow as high as six feet in some areas, while elsewhere they may be stunted and yield little seed cotton. Wilting through water-shortage is common, whilst there is evidence of waterlogging in some areas. Although there is much room for improvement in cultivation methods, crop development and yields must always remain to a certain extent uneven, owing to the system of irrigation.

Identity of the Species of *Diparopsis* in the Sudan.

Previous to 1951, the Sudan bollworm was known as *Diparopsis castanea* Hmps. The genus was revised by Clements (1951), who showed that the name *castanea* should be restricted to a species attacking cotton in Africa south of the equator, and that the species found north of the equator is a distinct one, which he named *perditor*. Specimens of *Diparopsis* from the Gash Delta have been identified at the British Museum (Natural History) as being of the latter species, which also attacks cotton in Nigeria (Geering & Baillie, 1954). Pearson (1954) has since pointed out that an earlier name exists for the species, which now should be known as *Diparopsis watersi* (Roths.).

* 1 kantar = 312 lb. approx.

Previous Work on *D. watersi* in the Sudan.

Diparopsis was first recorded in the Sudan, at Khartoum, in 1906 by King (1908), who gave a short account of its occurrence and life-history. The first full account of *Diparopsis* in the Sudan is that of Giffard (1929), who discusses in some detail its occurrence and various aspects of its biology at Shendi, Northern Province. In this account it is reported that *Diparopsis* was absent from Kassala in 1927. The date of its subsequent appearance is unknown, but Bedford (1936) refers to a "normal" infestation in the Gash crop of the 1934–35 season. Regular sampling of cotton bolls began in 1946 and, since that date, *Diparopsis* has been found to be the most numerous bollworm in the crop, accounting for approximately 75 per cent. of the total bollworm population over the years 1951–1955.

Observations at Shendi led to the conclusion that *Diparopsis* was originally univoltine in that district, with probably only an occasional, incomplete second brood. By 1926, it was found to breed throughout the cotton season in certain districts in the Northern Province (King, 1927). In the Nuba Mountains, as late as 1926, it was still reported as being univoltine (Giffard, 1929). Unfortunately, there is little information on the early history of *Diparopsis* in the Gash Delta, so it is not known whether it was ever univoltine in that area.

The Incidence of *D. watersi* during the Season.

The initial infestation of *Diparopsis* in the field in the Gash Delta arises from the emergence of moths from diapause pupae formed in previous seasons. Apart from the possibility of *Diparopsis* larvae feeding upon the growing points of the young cotton plants, the crop is not sufficiently advanced in growth to support an infestation of *Diparopsis* until the first flower buds appear, which does not occur on the X1730A variety until mid-October and not until mid-November on the later-sown Sakel. Prior to 1954, however, the more advanced ratoon cotton allowed an infestation to be established during September and, as this cotton was not cut out until towards the end of October, or in some cases not until November, it provided a source of infestation for the main crop. A typical curve showing the manner in which the crop is made is shown for variety X1730A in

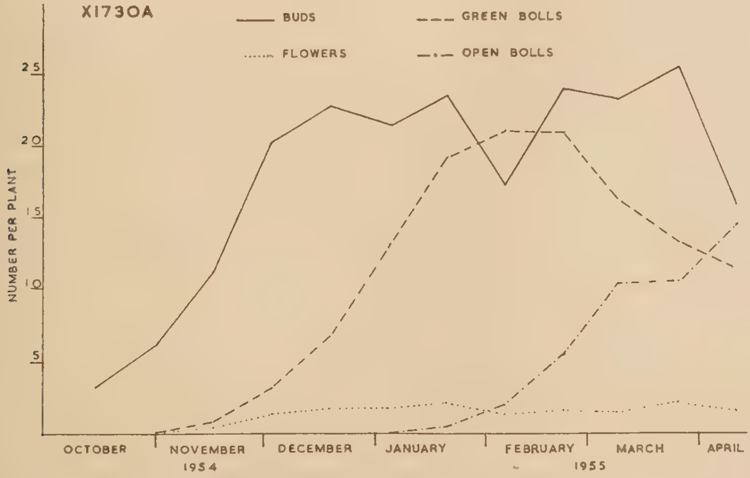

Fig. 6.—Production of flower buds, flowers and bolls, variety X1730A, 1954/55. Records show the numbers present per plant.

fig. 6. It should be noted that the April flowering does not contribute to the crop, the plants being cut out by 30th April or, if left, drying out.

Egg counts for the variety X1730A for the three seasons 1952–1955 are given in fig. 7. On this variety of cotton, egg-laying is initially heavier than on Sakel. During late November and early December, egg-laying is at a minimum. Generally from late December and January there is an increase, although

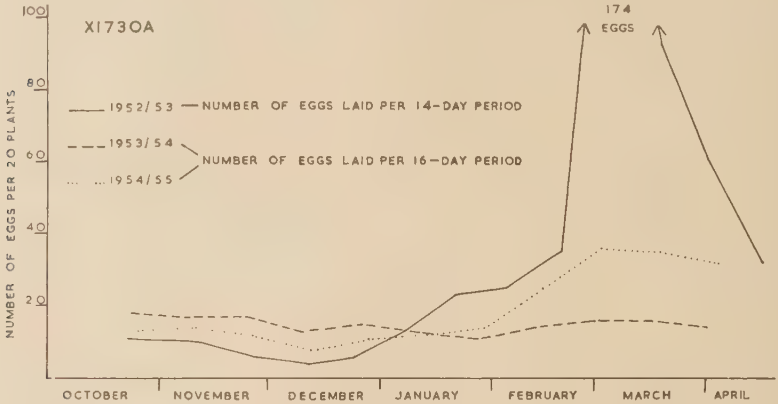

Fig. 7.—Egg populations of *Diparopsis watersi* on variety X1730A, in three successive seasons, 1952–55.

considerable variations occur between seasons. The decrease towards the end of the season is largely dependent upon the condition of the plants, egg-laying being maintained on those that still show active growth. Larval counts (fig. 8) show a general increase from the beginning of the season until the production of bolls begins to decrease. Maximum larval populations are reached rather later on

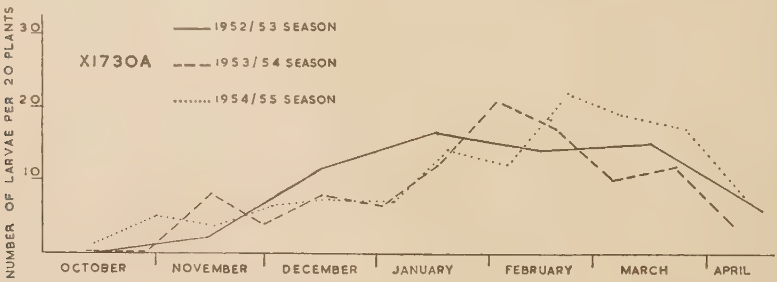

Fig. 8.—Larval populations of *Diparopsis watersi* on variety X1730A, in three successive seasons, 1952–55.

Sakel than on X1730A cotton. A more detailed account of the status and incidence of *Diparopsis* is to be given in a further paper. It may be noted, however, that in 1952–53, egg-laying was exceptionally heavy, and in that season the cotton plants were allowed to grow on longer than normally, in order to obtain the maximum crop. Larvae were present in the field in June, although in small numbers. Records were not continued after April, however, as owing to the irregular drying out of the fields, plant behaviour and consequently the incidence of *Diparopsis* likewise became irregular and counts would have been unreliable.

Breeding Experiments with *D. watersi.*

Information on the biology of *D. watersi* in the Gash Delta was obtained during the 1952–53 season by rearing successive generations in an outside insectary. This was a lean-to roof attached to the side of the laboratory. The sides were open, and thus temperatures would have approximated to air-shade temperatures. Rearing of the first generation commenced in early October 1952 with 100 eggs provided by moths caught in the field. It is probable that these moths had emerged from diapause pupae formed in previous seasons, as observations made during September indicated that it was too early for them to have been bred on ratoon cotton. The eggs for each subsequent generation were provided by four pairs of parents chosen arbitrarily from the non-diapause fraction of the preceding generation, each pair contributing 50 eggs. Thus, for each generation except the first, an attempt was madē to rear 200 larvae.

The moths selected for breeding were confined in lamp glasses, the females readily ovipositing on the muslin tops. The larvae were reared individually in small, wire-mesh cages partly sunk into soil contained in troughs. For the first generation, flower buds were stood in phials of water, but for subsequent generations only bolls were used, and it was found that they remained sufficiently fresh without water. The bolls were as large as possible without being dry and tough; their exact age was not known. The day before the eggs were due to hatch, one egg was placed underneath a bracteole on each boll, which was examined next day for penetration and, if necessary, reinfested. On fresh, green bolls with undamaged bracteoles, penetration took place, but old, mutilated bolls were often refused, and even if the larvae did penetrate successfully their development was usually very slow. The first boll normally sufficed for the larva until it reached the fourth instar or possibly the early fifth instar, when it would readily transfer to a fresh boll. Larvae reared in this manner appeared to be perfectly normal; when fully grown, they penetrated the soil and pupated. All the rearing was carried out in an outdoor insectary, except during the rains, when the cages were put outside to include the effect of rainfall on moth emergence.

For the rearing of the first generation, only flower buds were available and on this diet there was a heavy mortality of larvae while they were attempting to pupate. This probably arose through the larvae failing to reach full 5th-instar size; those that succeeded in pupating gave rise to very small moths with deformed wings. In the second and fourth generations, a high mortality also occurred because the moths that emerged from pupae that had been in diapause failed to escape through the heavy clay soil, which had baked hard following the rains. In the cages used for the third and fifth generations, the soil was lighter and the moths could pass through it easily. Losses in the fifth generation were due to larvae dying when about to pupate, perhaps as a result of the high air temperatures then prevailing. The figure for total diapause pupae, for those generations in which moths were found to be trapped in the soil, was reached by assuming that the trapped moths all represented diapause pupae. It was not possible to determine the distribution of emergence of such moths. An attempt to rear a sixth generation was unsuccessful. Egg viability was very low and the few larvae obtained could not be reared, owing to the poor quality of the bolls.

The results of the breeding experiments are summarised in Tables I and II, and they are discussed in detail later in this paper.

Observations on the Egg Stage of *D. watersi.*

The oviposition of *Diparopsis* has been little studied except by Smith (1933), who gives information on the oviposition of *D. castanea.*

On emergence from the pupa, the adult of *D. watersi* is sexually mature, and both mating and oviposition can occur on the night of emergence. To determine

whether the female moth shows any preference for a particular part of the plant on which to oviposit, eggs were recorded against the site of egg placement. The records were made in the field over the whole of the 1952–53 season, and are based on 9,405 eggs. The following proportions were obtained—leaves, 47·9%; flower buds, 36·5%; stems, 8·8%; flowers, 5·0%; and bolls, 2·0%. Twice as many eggs were found on the lower surface of leaves as on the upper surface. Most of the leaves bearing eggs were confined to the upper parts of the plant, the lower, older leaves tending to be avoided. Thus, nearly all the eggs were found on the younger and more accessible plant material. The figures show clearly that there is no preference for flowers or bolls. That moths will oviposit, for choice, on the more advanced plants was very apparent on ratoon cotton and on the main crop early in the season, when the larger plants always gave the higher egg counts.

TABLE I.

Results of breeding experiments, 1952–53.

	Generation				
	1st	2nd	3rd	4th	5th
Date eggs laid	5-6.x	8-12.xi	18-25.xii	2-6.ii	15-19.iii
Number of pupae formed ..	*46*	*158*	*133*	*151*	*97*
% diapause pupae ..	2·2	37·3	48·1	54·9	81·5
Incubation period	4	6	6	6	5
Larval period –non-diapause	14·6 (*45*)	12·6 (*99*)	14·5 (*70*)	12·8 (*68*)	12·3 (*18*)
	10–18	11–16	12–16	11–14	10–17
–diapause	16·0 (*1*)	12·9 (*51*)	15·1 (*64*)	13·1 (*82*)	12·4 (*79*)
	—	12–15	13–18	12–15	10–16
Pupal period –non-diapause	15·5 (*45*)	18·7 (*99*)	22·1 (*69*)	19·6 (*68*)	17·5 (*18*)
	13–29	13–27	19–33	17–24	15–20
–diapause	104·0 (*1*)	253·8 (*4*)	278·2 (*60*)	234·0 (*44*)	196·7 (*69*)
	—	76–322	236–305	141–291	125–309
Total life-cycle –non-diapause	34·1 (*45*)	36·3 (*100*)	42·6 (*69*)	38·4 (*69*)	34·8 (*18*)
	28–50	30–44	38–54	36–43	31–38
–diapause*	124·0 (*1*)	271·3 (*4*)	299·3 (*60*)	253·1 (*44*)	214·1 (*69*)
	—	93–339	257–325	159–310	141–326
Adult life, non-diapause–male	3·8 (*8*)	6·5 (*11*)	7·5 (*8*)	6·1 (*9*)	—
	3–5	3–9	4–10	5–7	—
–female	5·1 (*17*)	5·4 (*11*)	8·6 (*10*)	7·7 (*8*)	—
	3–7	3–7	6–11	6–9	—
Eggs per female	57 (*13*)	116 (*11*)	229 (*10*)	218 (*10*)	—
	3–144	54–192	166–283	109–275	—
Sex ratio (female/male)					
–non-diapause	1·8	1·3	1·0	0·8	0·8
–diapause	0·0	0·3	0·6	1·4	1·0

Periods are given in days. The figures given against each entry, except where otherwise stated, consist of the mean value, followed (in brackets and italicised) by the number of individuals on which the result is based, and with the range of values shown immediately below.

* These figures include only those pupae that gave rise to moths in the first season following pupation.

The number of eggs laid per female, together with the length of life of males and females under cage conditions, are given in Table I. Under these conditions, it was found that nearly 60 per cent. of the total number of eggs laid were produced during the second and third night following that of mating (Table III). The incubation period was observed to vary from four to six days and appeared to depend upon temperature.

Observations on the Larval Stage of *D. watersi*.

The length of larval life appeared to vary with temperature, reaching a maximum during the winter (Table I). There were five instars, all recognisable in the field.

Observations were made on the activity of larvae, especially those of the first instar from the time of hatching to the penetration of a bud, flower or boll.

TABLE II.

Distribution of moth emergences in 1953 from diapause pupae formed in the breeding experiment.

Emergences during 4-week periods starting on dates given (% of total emergences)						
–.ii	1.vii	29.vii	26.viii	23.ix	21.x	18.xi
1·1	1·0	0·0	9·1	56·6	27·7	4·5

3·8% of the diapause pupae still remained alive at the end of the first season's emergence.

Three experiments were set up in which it was possible to observe directly the path taken by a larva over the plant under different conditions of egg placement and plant growth. All observations were made in the laboratory on plant material freshly obtained. It was necessary to use torch light in following the path taken by the larvae, as hatching began at 3 a.m., but whether this had any

TABLE III.

Percentage of the total number of eggs laid on successive nights.

Day	1	2	3	4	5	6	7	8	9	10	11
%	*	6·1	28·4	29·4	16·5	10·1	4·9	3·0	1·1	0·0	0·5

* Mating took place.

effect on the larval behaviour is not known. In practice it was difficult to ascertain the exact instant of penetration, as at this stage the larva became hidden from view, and any disturbance of the plant was liable to affect its behaviour. Instead, it was decided to reckon the instant of penetration as that when the larva finally disappeared behind the bracteoles or the flower petals. Penetrations were checked later. During its wanderings a larva would occasionally reach the base of the plant stem, but rather than allow it to be lost it was replaced on the plant, at a point noted. It sometimes happened that a larva would drop by its attached thread, and unless it reached another part of the plant it was returned to the plant. A summary of the results of the three experiments is given in Table IV.

It will be seen that considerable wandering of the larvae occurred when eggs were placed on the terminal leaf of a sympodial branch (Experiment 1). In the majority of cases this resulted from the inability of the larva to locate the leaf petiole and so to leave the leaf lamina. With this placement of the egg it was

frequently noted that wandering occurred not only over the leaf lamina and other vegetative parts, but also over the outer and inner surfaces of the bracteoles, even though the larva might have contacted previously the surface of the bud or boll. Half the number of larvae observed, once they had located the leaf petiole, took the shortest route to the nearest bud or boll, namely, down the petiole and up the axillary fruiting stem. This route was short-circuited in some instances

TABLE IV.

Habits of first-instar larvae of *D. watersi*.

Experiment	Site of egg placement	Type of plant growth	No. of subjects	Average period of wandering (min.)	Range in period of wandering (min.)	No. larvae that penetrated		
						Buds	Flowers	Bolls
1	Terminal leaf of a sympodium	Vigorous; bud, flower or boll in the axil of each leaf	17	85	22–187	13	1	3
2	Terminal growing point of a monopodium	Vigorous; bud, flower or boll in the axil of each leaf	15	27	3–54	15	—	—
3	Terminal growing point of a monopodium	Not vigorous; plant material taken late in the season	19	19	5–75	18	1	—

where a bud or boll happened to be in contact with the leaf. It was noticed on two occasions that, after excessive wandering, the larva appeared to rest for approximately 20 minutes, following which normal wandering was resumed. Some of the larvae, again only after excessive wandering, distributed themselves on attached threads.

When eggs were placed on the terminal growing point of a monopodial branch, the period of wandering was lessened considerably. Over half the larvae observed confined their wandering to the growing point and adjacent buds, and the majority chose one of the four or five buds nearest to the site of egg placement. Unlike the larvae in Experiment 1, these wandered little over the surface of the bracteoles once a bud had been reached, perhaps because they had not been wandering excessively beforehand. The difference between Experiments 2 and 3 in respect of the average period of wandering was probably because the larvae were less hampered by foliage in the latter experiment. Another experiment showed that when eggs were placed on either the inside or outside surfaces of bracteoles, the enclosed bud or boll was invariably penetrated, with little or no wandering over the plant surface. Penetration of a bud or boll was always made at a point where it was in contact with one of the bracteoles, the larva previously joining the two surfaces together with a small web.

The above observations showed that the period of wandering, from the time of hatching to the penetration of a bud or boll, was dependent to a large extent upon the placing of the egg and the type of plant growth. In the majority of cases, with normal egg placement amongst the young foliage and buds, little wandering took place and the larva quickly found a bud. The fact that larvae are able to distribute themselves by means of an attached thread may be of importance in the field, but under laboratory conditions this method of dispersal

was only resorted to after excessive wandering. The larvae were never observed to feed on parts of the plant other than buds, flowers or bolls and on bolls they always discarded the outer rind. Little mortality resulted from larvae failing to find a suitable bud or boll and it is concluded that such mortality is negligible on actively growing plants. It was not determined at which stage the larva spins the web across the point of abscission of a bud or boll. The presence of this web is a very noticeable feature of attack by *Diparopsis* and it has always been considered to be formed during the course of initial wandering. However, this does not seem to be the case, and it appears that the web is formed at some later stage, perhaps when the larva finally leaves the bud or boll in search of further food. In the experiments, the larvae did not show any preference between buds, flowers or bolls, selecting whichever was nearest to the site of egg placement, which on a normal healthy plant was usually a bud. It was noticed that the very small buds tended to be avoided, owing no doubt to the difficulty in penetrating between the closely knit bracteoles.

Observations on the Pupal Stage of *D. watersi.*

The larvae of *D. watersi* normally pupated in the soil, although on occasions pupae were found within bolls. The way in which a larva that is about to pupate leaves the plant was not determined, but a number of observations were made on the habits of larvae on entering the soil and on subsequent pupation and moth emergence.

Method of entering the soil.

In loose soil, the larvae were found to penetrate at any point, but in a normal Gash soil, where the surface layers are hard, penetration was usually by way of a crack. On reaching pupation depth, each larva excavated a small cavity in which the cocoon was made, often in the side of the crack. The depth of the cavity was sufficient to allow the anterior end of the cocoon to protrude slightly. Larvae tunnelled into the hardest of soils in this manner. In only one or two instances were larvae observed to penetrate a hard soil other than by way of a crack.

TABLE V.

Depth of pupation for different types of soil.

Soil type	No. of pupae	Percentage of pupae at varying depths (in.)			Remarks
		0–1	1–2	2–4	
Light soil, broken and loose	130	63·0	30·0	7·0	Measured at one-inch intervals
Light soil, overlaid with a hard pan of silt	164	89·6		10·4	Measured at two-inch intervals
Light soil, overlaid with a hard pan of silt	30	80·0	20·0	0·0	Each pupa measured individually
Heavy soil, deeply cracked	77	82·0		18·0	Measured at two-inch intervals
Heavy soil, surface layer well cracked	47	95·8	4·2	0·0	Each pupa measured individually

Depth of pupation.

The depth of pupation was measured for different soil types (Table V).

Table V shows that very few larvae pupated at a depth greater than two inches in any type of soil, the majority pupating at a depth no greater than one inch. Where it was possible to measure the depth of the pupae exactly, up to 25 per cent. were found within the top half-inch of soil. No pupa was observed below three inches. It is possible that those pupae recorded at the 2–4 in. depth interval, when the measurements were made at 2-in. intervals, were accidental inclusions from the top two inches of soil. The results do not provide any evidence to suggest that depth of pupation varies with soil type to any great extent.

Length of time between penetration of the soil and the formation of the cocoon and pupa.

Construction of the cocoon began immediately the larva reached the depth of pupation and it appeared that, in a loose soil, it was completed by the following day. The formation of the pupa did not occur until the fifth day following penetration into the soil.

Emergence of moths.

A number of observations was made concerning the ability of moths to escape through soils of different types. A moth emerging from a non-diapause pupa is presumably able to follow the path originally taken by the larva when entering the soil, and it thus encounters little difficulty. On the other hand, moths emerging from diapause pupae may encounter soil conditions very different from those that existed when pupation occurred since, in most cases, the path taken by the larva will have been obliterated by rain. In order to reach the surface these moths, therefore, have to pass through a compacted layer of soil, which may be either saturated with water or baked hard. It was observed that moths escape through at least three inches of wet clay soil, so little difficulty is likely to be experienced by moths emerging under natural conditions during the rains. When the soil has hardened after the rains, the moths experience greater difficulty. In a heavy clay soil they were unable to travel for any distance, and were usually found dead with the abdomen still enclosed within the pupal case. In a lighter soil, however, they were able to travel a distance of up to two inches. The method by which the moths actually pass through the soil is not known, but since they leave well-defined tunnels, it would seem that they must bore through the soil and do not merely push their way.

The Pupal Diapause in *D. watersi*.

Experiments were carried out to determine what proportion of larvae form diapause pupae during the season, and the periods over which emergence from diapause pupae occurs, together with the relative magnitude of the emergence from each if there proved to be more than one.

Pupation experiments using cages.

Fifth-instar larvae were collected from the field and allowed to pupate in suitable cages and the subsequent emergence of moths recorded.

(i) *Experiments under laboratory conditions.*—Pupation cages were set up on 5th March, and 7th and 21st April 1953, each containing approximately 100 pupae. Table VI gives the proportion of larvae that formed diapause pupae, together with the distribution of emergences from these pupae. Calculations are based on recorded emergences and on the numbers of pupae that were still alive

when the cages were examined in August 1954. Total mortality in the cages was 16·3 per cent.

The distribution of the emergences was not dependent to any extent on the date of pupation and it was markedly unimodal in character. This experiment was carried out under more constant conditions of temperature than occur in the field, the temperature never having risen above 32° or fallen below 20°C.

(ii) *Experiments under field conditions.*—Experiments under field conditions were set up during each of the three seasons 1951–52, 1952–53 and 1953–54, but only from the last were reliable results obtained. During 1951–52, fifth-instar larvae were difficult to obtain and few cages could be stocked, also ants were troublesome and destroyed many of the larvae and pupae. In 1952–53, although a very large number of larvae was collected, a heavy mortality resulted amongst the moths because they failed to escape through the heavy clay soil after it had baked hard following the heavy rains in 1953. A lighter soil was used in the cages set up in 1953–54.

The cages used in the last two seasons' experiments measured 28 × 9 × 9 in. and were made of sheet tin except for the top and bottom which were of wire mesh, the former embodying a sleeve. When sunk into the ground to a depth of 22 in., the cages projected 6 in. above ground level and, if the exposed sides were kept clean, they proved to be satisfactorily antproof. The cages were stocked with bolls containing fifth-instar larvae at the rate of 100 bolls per cage, care being taken to leave the larvae as little disturbed as possible. As long as infested material was available in the field, five cages each week were stocked. At the end of each week the cages were cleared of boll débris, together with any larvae that had failed to pupate. In 1952–53, provision was made to shade the cages during the time cotton was standing in the field, in an attempt to simulate field conditions. It was doubtful, however, whether this could be done efficiently, especially as the cages were shielded to a certain extent by the sides and mesh top, and shading was discontinued in 1953–54.

In order to minimise the loss of information that might arise through failure on the part of the emerging moths to reach the surface under certain soil conditions, a number of cages of the 1953–54 experiment was examined before and after the rains and also when moth emergence for the season had ceased in March. These three examinations showed little moth mortality, the total mortality percentages being 17·6, 26·7 and 21·9, respectively.

The results of the pupation experiment started in 1953–54, in which approximately 4,000 fifth-instar larvae were allowed to pupate, are summarised in Table VII, and are based on the moths that emerged plus pupae still alive and in diapause. The mean mortality figure of 22·1 per cent. used in the analysis was obtained by the examination of only 60 per cent. of the pupation cages, as it was necessary to leave the remaining cages undisturbed for recording the moth emergences over further seasons. Data giving these emergences are not yet available.

The proportion of larvae that formed diapause pupae tended to increase as the season advanced and the distribution of emergences from diapause pupae appeared to be independent of the date of pupation, as in the case of the laboratory experiments. There was, however, a marked bimodal distribution of emergences in the season following that of pupation, and a high proportion of pupae still remained in the soil after the first season's emergence. These results are supported by those of the experiments started in 1951–52 and 1952–53, in which moth emergence was distinctly bimodal, with peak periods of emergence in August–September and December–January. These earlier experiments also showed that some pupae remained in the soil sufficiently long to give rise to moths over a further two seasons, so that emergence from a given lot of pupae may extend over three seasons.

TABLE VI.

Distribution of moth emergences in 1953–54 from diapause pupae formed in 1953 and kept under laboratory conditions.

Date of pupation	Total live pupae formed	Pupae in diapause (%)	Emergences during 4-week periods starting on dates given (% of total)										Not emerged
			1.vii	29.vii	26.viii	23.ix	21.x	18.xi	16.xii	13.i	10.ii	10.iii	
5.iii.53	218	36·7	5·0	27·5	45·0	17·5	1·3	—	—	3·8	—	—	—
7.iv.53	260	17·7	6·5	26·1	43·5	10·9	8·7	—	—	—	2·2	—	2·2
21.iv.53	414	80·7	6·0	18·6	39·8	15·0	3·3	1·8	0·9	1·8	4·5	1·2	7·2
Total	892	51·6	5·9	20·9	41·1	15·0	3·5	1·3	0·7	2·0	3·5	0·9	5·4

Emergences calculated as % of total moths emerged + pupae not emerged but still alive in August 1954.

TABLE VII.

Distribution of moth emergences in 1954–55 from diapause pupae formed in 1953–54 and kept under field conditions.

Month of pupation	Pupae in diapause (%)	Emergences during 4-week periods starting on dates given (% of total)								Not emerged
		28.vii	25.viii	22.ix	20.x	17.xi	15.xii	12.i	9.ii	
December 1953	4·4	—	—	27·8	—	—	55·6	—	—	16·7
January 1954	30·6	0·3	20·3	12·6	0·7	9·3	13·4	3·1	0·3	40·0
February 1954	39·8	0·5	9·3	13·6	2·1	3·7	25·9	15·7	0·6	28·5
March 1954	43·7	0·9	14·7	12·9	0·4	9·0	13·1	9·3	0·9	38·8
Weighted means	35·7	0·6	14·6	13·1	1·1	7·2	18·0	9·5	0·6	35·4

Emergences calculated as % of total moths emerged + pupae not emerged but still alive.

Sampling for pupae in the field.

Soil sampling for pupae of *D. watersi* on two areas sown to cotton in 1952 was carried out during the dead season (May–June) in 1954 and in 1955 (Table VIII).

TABLE VIII.

Density of diapause pupae in the soil.

Area	No. of square-metre samples	No. live pupae per sq. m.	
		1954	1955
Degein 24W	600	0·063	0·033
Hadaliya 10A	200	0·244	0·015

The figures give only the approximate density, but they support the results of the field pupation experiments in showing that pupae remain alive in the soil for at least three seasons.

Rearing successive generations of D. watersi.

In rearing successive generations of *D. watersi* in an outside insectary (see p. 9), it was found that the proportion of larvae that formed diapause pupae increased with each successive generation, reaching approximately 80 per cent. in the fifth (Table I). The distribution of moth emergences from the diapause pupae was distinctly unimodal (Table II) and there was no evidence to show that the period of emergence varied with date of pupation, and thus with generation.

Information from egg counts.

Counts of egg-laying by *D. watersi* in the crop do not provide a great deal of information on the emergence of moths from diapause pupae, as they are, obviously, dependent to a considerable extent upon the amount of breeding that has occurred in the crop, the number of plants available for oviposition and the activity of the moths. Egg counts on ratoon cotton showed, however, that when this started growth at the end of August there was already an emergence of moths in progress and further counts, on X1730A and Domains Sakel cotton, showed that there was a decrease in the rate of emergence during November and early December.

Discussion on the Pupal Diapause in *Diparopsis*.

The proportion of larvae of *D. watersi* that formed non-diapause pupae decreased as the season advanced or, as the generation experiment showed, with successive generations, but at no period of the season was a complete cessation in the production of such pupae observed. In 1953, fifth-instar larvae collected from the field at the beginning of June, eight months after larvae had first appeared in the crop, were still producing non-diapause pupae, and under cage conditions it was demonstrated that these pupae were being produced in the fifth generation to the extent of 20 per cent. of the pupal population. The persistence of the *Diparopsis* infestation is noteworthy, for Geering & Baillie (1954) have shown that, in Nigeria, six months after the first emergence of moths from diapause pupae and only two months after the final emergence, there is a complete cessation in the production of non-diapause pupae.

The bimodal nature of the emergence of moths from diapause pupae appears

to be a common feature of *Diparopsis* biology, its occurrence having also been demonstrated in both Nyasaland (Pearson & Mitchell, 1945) and Nigeria (Geering & Baillie, 1954). It now seems fairly certain that this pattern of emergence is the result of modification by certain environmental factors of a more basic unimodal distribution. There is a considerable body of evidence in support of this contention. In the Gash Delta it was shown that when diapause pupae were kept in the laboratory and thus exposed to more constant conditions than would be the case in the field, the subsequent emergence of moths was essentially unimodal in form. Similar results have been obtained in both Nyasaland and Nigeria from experiments conducted in a constant environment. Thus it becomes important to determine the factors responsible for the bimodal emergence in the field, for without the extension of the emergence into two main periods, the bulk of the emergence in the three regions would occur before the cotton plants were able to support an infestation. If the factors proved to be capable of alteration or elimination then there would be a distinct possibility of reducing the importance of *Diparopsis* as a pest of cotton. At present, the second period of emergence enables a considerable proportion of the carry-over moth flight to contribute to the new season's infestation. This is particularly true of the Gash Delta, where it has been shown that this emergence occurs at a time when the crop is probably able to support the maximum bollworm population, namely during December and January.

Pearson & Mitchell (1945) found that diapause development in pupae of *D. castanea* was suppressed at temperatures above 36° or below 19°C., and also when the soil became waterlogged. In Nyasaland, one period in which suppression of emergence occurs is during the rains, and Pearson & Mitchell were able to show that it could be accounted for by waterlogging of the soil, the soil temperatures not being inhibiting at that time. Geering & Baillie were able to account for the bimodal emergence in Nigeria in a similar manner. This explanation, however, cannot account for the bimodal distribution of emergence in the Gash Delta, for it is not until the rains have finished that there is any suppression of emergence, and indeed, it is during the rains that the first emergences occur. The rainfall in the Gash Delta is unlikely to have any great effect on pupal development, for it is very light, compared with Nyasaland or Nigeria, and little or no waterlogging results. Nevertheless, little emergence occurred (Table II) in

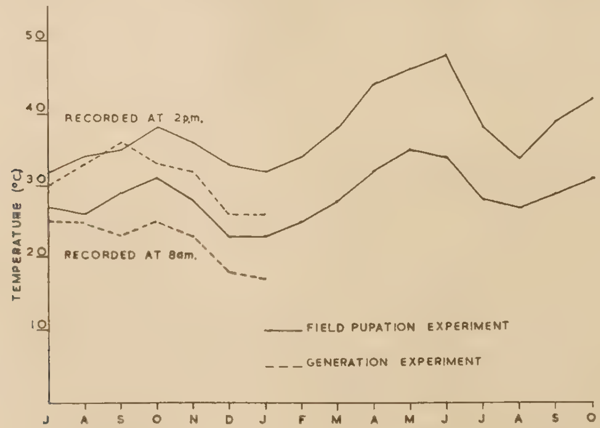

Fig. 9.—Mean daily minimum and maximum soil temperatures at a depth of 2 in. (recorded at 8 a.m. and 2 p.m., respectively). Aroma, 1953–54.

the generation experiment until the rains had practically ceased, at the end of September. This is in contrast to the results of the laboratory (Table VI) and field-pupation (Table VII) experiments, in the first of which, in particular, there was a considerable emergence before that date. There was, thus, in the generation experiment, a factor that operated towards suppression of emergence during September. Temperature may be ruled out, because the cages were placed in the open to include the effect of rainfall over this period, and soil temperatures were thus little different from those prevailing in the field pupation cages (fig. 9). However, it was noticed that the soil in the troughs containing the cages became waterlogged, despite attempts at drainage, and this factor is considered to be what suppressed emergence during September. Thus, were rainfall higher in the Gash Delta, waterlogging might play a part in suppression of moth emergence.

In the generation experiment, cages were returned to the insectary towards the end of September, and there was an immediate emergence of moths which continued until the middle of December, reaching a maximum during October and the first half of November. Emergence was unimodal and indicated that the return of the cages to the insectary resulted in the elimination of some factor that was by then suppressing emergence in the field. The only factor that altered considerably in the generation experiment cages was that of soil temperature, which had fallen immediately they were returned to the insectary. In the field-pupation cages, on the other hand, soil temperatures were rising at that time, following the end of the cool weather that prevails during the rains. Pearson & Mitchell (1945) showed that when temperatures reach a certain level (36°C. in the case of *D. castanea*), pupal development is inhibited. Fig. 9, giving soil-temperature data, shows that over the period October and November temperatures were well below this critical value in the cages of the generation experiment, while in those of the field-pupation experiment, temperatures were probably sufficiently high to suppress pupal development. Thus, in the former experiment, soil temperatures were insufficient to suppress emergence, and a unimodal distribution resulted. In the pupation cages, soil temperatures did not fall to any extent until December, when emergences recommenced and continued until temperatures rose in February. From March until July, temperatures remained very high, and there was a complete cessation of emergence during this period. There is, therefore, evidence to suggest that the bimodal distribution of the emergence of *Diparopsis* in the Gash Delta is largely a result of high temperatures inhibiting pupal development over certain periods of the season.

It was shown, both from pupation experiments and from sampling for pupae in the field, that the emergence of moths from diapause pupae was not completed during the season following that of pupation, but extended over at least two further seasons. The high proportion (approximately 35%) of the diapause pupae that remains in the soil following the first season of emergences is a new feature in known *Diparopsis* biology and, at present, appears to be unique to the Gash Delta. In both Nyasaland and Nigeria, emergence is virtually complete by the end of the first season (Pearson & Mitchell, 1945; Geering & Baillie, 1954). At Shendi, Giffard (1929) recorded pupal periods of up to 13 months, but did not indicate whether there was any substantial carry-over to a second season. The pupation experiments gave no indication of any differences between the seasons as regards the pattern of emergence, and it may be assumed that, in each season, the emergence of moths from diapause pupae follows the bimodal pattern previously described.

The multimodal distribution of moth emergence from diapause pupae in the Gash Delta may be explained in a similar manner to that of the bimodal distribution of emergence in any one season, namely, high temperatures inhibiting pupal development. Rainfall may have a direct effect on emergence, especially in some seasons, although in the Gash Delta its main function would probably be to

lower soil temperature through evaporation rather than to suppress pupal development by creating waterlogged conditions. Depth of pupation and soil type have also to be considered but, again, their effect would probably be indirect inasmuch as soil temperature would be dependent upon them. It is difficult to see how relative humidity of the air could effect emergence, considering the complete isolation of the pupa within its cocoon. The extended emergence of *D. watersi* strongly indicates that conditions favourable to pupal development are always of short duration, and if climatic changes determine the emergence, all seasons are unlikely to be equally favourable to emergence. The result of this would be to vary the proportion of diapause pupae giving rise to moths over each of the seasons contained within the overall emergence period, and thus to effect a build-up of pupae in the soil. This would provide an explanation for the unusually heavy attack of *Diparopsis* during the 1952–53 season, which at the time was difficult to account for, the previous season being one of low bollworm incidence. It is significant that during the rains of 1951 the mean daily maximum temperatures never fell below 37°C.

Natural Mortality of *D. watersi*.

Collection of eggs from the field failed to reveal the presence of any egg parasites, which thus, if present, must exert little controlling influence. Egg predators, likewise, were never observed, and egg fertility was generally high. However, eggs obtained in the laboratory towards the end of the season often failed to hatch, even though the embryo developed fully, and high temperature is thought to be a likely explanation.

When plants bearing reasonable numbers of buds and bolls were infested with eggs, first-instar larvae encountered little difficulty, after eclosion, in finding suitable food and the rate of survival appeared to be high under such conditions. A scarcity of buds and bolls, on the other hand, such as might occur after a heavy bollworm attack, would be likely to increase mortality considerably. Nothing is known of the effect of availability of food supply on the survival of later instars. Towards the end of the season it became noticeably more difficult to rear larvae in the laboratory, despite the availability of young bolls, and it is suggested that unfavourable climatic conditions, such as high temperatures, were responsible.

The parasite, *Apanteles* sp. (*ultor* Reinh. group), was found to be common throughout most of the season and attacked the earlier instars of *D. watersi*. Its presence in the field was made readily noticeable by the small, white, pupal cocoon attached to a bud or boll near the site of entry of its bollworm host. From this it appeared that the bollworm was parasitised soon after the initial bud or boll penetration, or when wandering in search of fresh food. This parasite was also found to attack *Earias insulana* (Boisd.).

A species of *Bracon*, probably *brevicornis* Wesm. was observed as a common parasite of the later instars of *Diparopsis*. The bollworm normally succumbed to the attack of the parasite when about to leave the bud or boll to pupate, and the parasite larvae, of which there were several to each host, were thus able to pupate on the plant itself. A characteristic feature of the attack of the parasite is the black discoloration which often appears on the skin of the bollworm host. *B. brevicornis*, which also parasitises larvae of *E. insulana*, is undoubtedly of considerable importance in controlling *D. watersi*, especially in the latter half of the season. In March 1954, fifth-instar larvae on one area of cotton were found to be parasitised to the extent of 20 per cent.

Apanteles earterus Wlkn. attacked third-instar larvae of *D. watersi*, but it was not common.

Sturmia (*Prosturmia*) *imberbis* (Wied.) although of great importance in

controlling *Heliothis armigera*, did not parasitise *D. watersi* to any extent. It attacked the later instars.

The only predators that were observed to attack the larvae of *D. watersi* were Neuropterous larvae, and ants. The former were very abundant at times on the cotton plants, and are considered to be of importance. Ants attacked fifth-instar larvae as the latter entered the soil to pupate, but they were never known to attack larvae feeding on the plant. Ants were also the only insects observed to destroy pupae.

Conclusions.

The study of the biology of *D. watersi* has in many ways emphasised the difficulties of controlling this pest of cotton. A control of the initial infestation in the crop would not be effective in reducing the population to a low level throughout the season, as it would be largely offset by the second emergence of moths from diapause pupae in December and January. This second emergence, unlike the first, occurs at a time when the plants have sufficiently matured to suffer a direct loss of crop through attack on the boll. Moreover, this emergence is so late as to allow the plant no time in which to recover from the attack and to set a fresh crop, unless the length of the "dead" season were to be considerably reduced, a practice which is on no account to be recommended, because of the likelihood of an increased carry-over moth flight.

It is not to be inferred that control of the initial infestation is entirely without value; on the contrary, a measure that would reduce this infestation and thus enable the plants to set their bolls at the earliest possible date is to be encouraged. It has been shown that much of the first emergence of moths occurs too early in the season to infest the cotton crop directly and, with the elimination of ratoon cotton, this emergence becomes largely ineffective. The seasonal flow of the River Gash prevents any alteration of the sowing date, and even if an alteration were possible, it is doubtful whether the infestation could be materially reduced, as any benefit from later sowings would be offset by the delayed maturation of the crop. There is, however, a case for discontinuing the recent practice of sowing a few first-rotation fields before the middle of August. Such fields always suffer from a very heavy initial attack, and no doubt provide an additional source of infestation for those sown later. The use of insecticidal dusts or sprays to control the initial infestation can hardly be justified economically in view of the infestation arising from the second emergence of moths. This later infestation would be most difficult to control in a similar manner, owing to the advanced state of growth of the plants. It may be noted here that if insecticides are ever to be used to control the initial infestation, the effect that they may have on the natural mortality of *Diparopsis* would have to be most carefully considered. Certain parasites, notably *Apanteles* sp. and *B. brevicornis*, are undoubtedly of importance in controlling *Diparopsis*, and any reduction in their numbers through the use of insecticides early in the season would be likely to favour the build-up of bollworm following the second moth emergence.

The extended period of moth emergence from diapause pupae greatly reduces the effectiveness of any control measure directed at the egg, larval and adult stages, for it means that at no time is it possible to attack the entire population. Clearly then, the most effective control of *Diparopsis* is to be obtained by the destruction of diapause pupae, preferably during the "dead" season, when all the other stages are completely absent. In this way the magnitude of each emergence period would be equally reduced. The fact that the majority of pupae occurs within the top two inches of soil suggests the use of mechanical cultivators, such as disc ploughs and disc harrows, as a measure of control based on physical destruction of pupae. This practice would, in addition, serve well the agricultural interests of the Gash Delta. Preliminary experiments carried out over the

1954–55 season indicated that disc-ploughing to a depth of eight inches effects a 50 per cent. reduction in pupal population.

A different measure of *Diparopsis* control was suggested by Geering & Baillie (1954), namely, the production of a unimodal emergence from the diapause pupae in the field. This should result in the main emergence occurring before the cotton plants are able to support an infestation, as was exemplified by the unimodal emergence obtained in the laboratory pupation experiments. The possibility of such a control measure will not be known, however, until the factors affecting the emergence of moths from diapause pupae are more perfectly understood.

Climatic conditions in the Gash Delta and Nigeria are dissimilar and thus it is not surprising to find that the biology of *D. watersi* differs to a certain extent in the two regions. In contrast to Nigeria, there is no abrupt cessation in the production of non-diapause pupae, and infestations persist as long as there is actively growing cotton. The remaining differences, namely, those observed in the pattern of emergence from diapause pupae, are thought to be the result of dissimilar environmental conditions modifying a basic unimodal distribution of emergence common to *D. watersi* in both the Gash Delta and Nigeria.

Summary.

Diparopsis watersi (Roths.) is a serious pest of the cotton crop in the Gash Delta of the eastern Sudan. The climate and method of cotton cultivation are described briefly and a general account of the incidence of *D. watersi* during the season is given. Earlier work in the Sudan on this bollworm was mainly centred in the Northern Province and there is little information on the history of its occurrence in the Gash Delta. The aspects of its biology considered here include its egg-laying and larval habits, and duration of the pupal stage.

The majority of eggs were laid on the younger and more accessible plant growth. The period of wandering in search of food after eclosion from the egg was of short duration with normal egg placement, the emerging larvae had little difficulty in finding suitable food, and mortality from failure to do so was low on healthy plants. Depth of pupation did not vary greatly with soil type; the majority of pupae were found within one inch of the soil surface, and none at a depth greater than three inches. Only when the soil was a heavy clay that had baked hard following the rains, did the emerging moths have difficulty in passing through it and ascending to the surface.

The proportion of larvae forming diapause pupae increased amongst field-collected larvae as the season advanced, and in successive generations bred in an insectary from the non-diapause fractions of the preceding generations, but at no time was there a complete cessation in the production of non-diapause pupae and infestations persisted as long as there was actively growing cotton. This persistent activity in the Gash Delta is contrasted with the restriction of *D. watersi* to a six months' season in Nigeria. The emergence of moths from diapause pupae was not completed during the season following that of pupation, but extended for at least two further seasons; approximately 35 per cent. of the total diapause pupal population was still alive and present in the soil after the first season's emergence. In any one season the emergence was bimodal, the two peaks of emergence, which were of similar magnitude, occurring in September–October and mid-November to mid-January. When diapause pupae were kept in the laboratory and thus exposed to less extreme temperatures than in the field, the emergence was distinctly unimodal, with maximum emergence during September. The bimodal emergence observed in the field is considered to be a result of external environmental factors that inhibit pupal development at certain times of year, and emergence data from diapause pupae exposed to different climatic conditions suggest that high soil temperatures are such a factor. The pattern of

moth emergence from diapause pupae in the Gash Delta is compared with that found in Nigeria and Nyasaland.

Natural mortality of *D. watersi* is discussed, and certain larval parasites, notably an un-named species of *Apanteles* of the *ultor* Reinh. group, and *Bracon brevicornis* Wesm., are considered to be of importance.

The study of the biology of *D. watersi* has emphasised the difficulties in controlling this bollworm, and stressed the importance of attempting to destroy it in the diapause state, preferably during the " dead " season. It is considered that mechanical cultivation of the soil may provide a means to that end.

Acknowledgements.

The author wishes to acknowledge the assistance of his colleagues, Mr. E. Dennis and Mr. E. Wright. Their investigations, which receive little specific reference in the present paper, have provided extensive data on bollworm populations. The author expresses his thanks to the Chief of the Research Division, Ministry of Agriculture, Sudan, for permission to publish this paper and to Mr. R. J. V. Joyce for his continued help throughout the investigations. Thanks are also due to Mr. H. W. Bedford, Mr. G. C. O'Farrell, Mr. J. Steven, and Mr. E. O. Pearson for reading and suggesting amendments to the draft.

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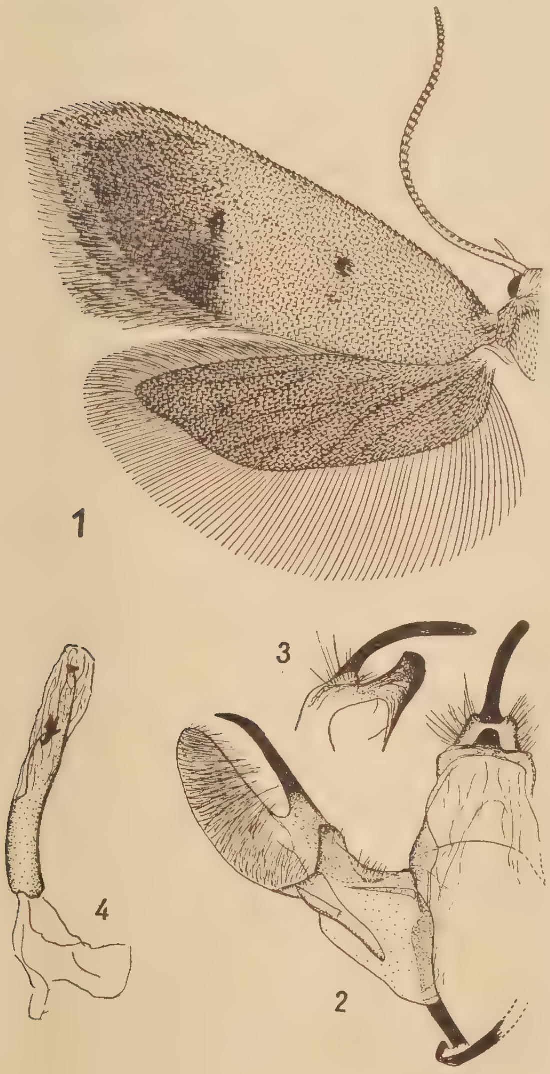
A NEW SPECIES OF XYLORYCTID MOTH BRED FROM COFFEE IN EAST AFRICA.

By J. D. Bradley
British Museum (Natural History).

Investigations by Mr. D. J. McCrae of the Coffee Research Station, Ruiru, Kenya, have revealed the existence of a species of the Microlepidoptera the larva of which feeds on the fruits of the coffee tree, *Coffea arabica*. It is an apparently undescribed species belonging to the genus *Odites* Walsingham (*sens. lat.*), which



Figs. 1–4.—*Odites semibrunnea*, sp. n. (1) Wings of adult male. (2–4) Male genitalia: (2) ventral view; (3) ventrolateral view of uncus and gnathus; (4) lateral view of aedoeagus.

is represented in Africa by more than 50 species, of which about ten are found in East Africa.

The species is described below from material bred by Mr. McCrae, and we are indebted to him and the Commonwealth Institute of Entomology for allowing the type and paratypes to be deposited in the British Museum (Natural History).

Odites semibrunnea, sp. n. (Figs. 1–4.)

♂. Expanse 14–15 mm. Labial palpus, head, thorax and tegula pale honey-yellow, crown of head somewhat shining, tegula suffused with dark brown except at tip. Antenna and scape honey-yellow, apical 3/4 of antenna suffused with greyish and with the dorsal side of each segment marked with dark brown at the base. Forewing: ground colour honey-yellow (or a shade of burnt sienna); basal 3/5 sometimes with a weak admixture of brownish, distal 2/5 solidly overlaid with dark brown except sometimes at apex where a trace of ground colour may be evident, base of costa dark brown and anterior edge irrorate with dark brown, a small conspicuous jet-black dot at 1/3 a little above middle, sometimes a vestige of a similar dot a little below, a heavy jet-black dot at about 3/5 in middle and at the edge of the dark brown distal area, cilia honey-yellow from costa to near tornus thence greyish fuscous. Hind wing greyish fuscous. Abdomen fuscous above, fuscous with an admixture of ochreous below. Legs ochreous heavily overlaid with fuscous.

Male genitalia (figs. 2, 3 and 4): The comparative length and development of the free costal part of the valva, and the long, slender, curved uncus are important diagnostic characters.

Type ♂: "Kiambu, Njuno Estate, xi.1956. *ex. C. arabica* fruits (*D. J. McCrae*)." Paratypes 3 ♂♂: same data as type. Genitalia slides 4806, 4658.

This species is a close relative of *hemipercna* Meyrick which occurs in Nyasaland; the markings on the forewing in both species follow the same general pattern but in *hemipercna* the coloration is much paler and it is a smaller species having a wing expanse of 10 mm.

The illustration of the wings of the adult (fig. 1) is reproduced from a drawing by Arthur Smith.

A MORPHOLOGICAL COMPARISON OF THE ADULTS OF *ORYZAEPHILUS SURINAMENSIS* (L.) AND *O. MERCATOR* (FAUV.) (COL., CUCUJIDAE).

By JOAN M. SLOW.*

Oryzaephilus mercator (Fauv.) was described as a new species by Fauvel (1889), who distinguished it from amongst material then regarded as *O. surinamensis* (L.) by the following characteristics:— longer, narrower head; large eyes reaching almost to the posterior angles of the head, the temples being reduced to a tooth; the penultimate joint of the antennae wider in comparison with its length; the grooves on the pronotum more parallel and often narrower; the elytra longer and narrower, with the margin less sinuate behind the shoulder. Grouvelle (1913) using only the ratio of length of eye to length of temple as a distinguishing character, claimed to have found a series of eye/temple ratios, of which *surinamensis* and *mercator* were extremes. As a result there has been some doubt as to the status of *O. mercator* although it has usually been regarded as a distinct species (Hinton & Corbet, 1943; Zacher, 1942). The object of the work described in this paper, in conjunction with that described by Howe (1953, 1956), was to decide by morphological and biometric methods whether or not these were true species and to discover if cross-breeding were possible.

General Description.

The adult of *O. surinamensis* is generally about 3 mm. long, but ranges from 2·75 to 3·25 mm. *O. mercator* is in general larger and darker than *O. surinamensis*, the length being normally about 3·25 mm., ranging from about 3 to nearly 4 mm.

Head.

The head of *O. surinamensis* (fig. 1,a) is broad at the temple, just behind the eyes, narowing anteriorly, and with a narrow portion behind the temples. The temples (ts) are about two-thirds of the length of the eyes, measured longitudinally. The eyes are black, round and convex. There are about 30 to 40 large ommatidia, with short fine hairs between them.

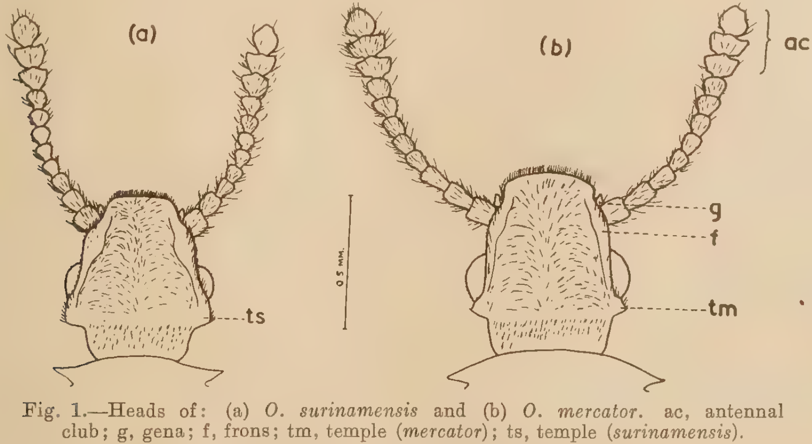


Fig. 1.—Heads of: (a) *O. surinamensis* and (b) *O. mercator*. ac, antennal club; g, gena; f, frons; tm, temple (*mercator*); ts, temple (*surinamensis*).

* Now Mrs. J. M. Wells.

In *O. mercator* (fig. 1,b) the head is more parallel-sided than in *O. surinamensis*, but it tapers slightly towards the front. The temples (tm) are small and tubercular in form. The eyes are very large, about three or four times the length of the temples and consist of about 40 to 50 large ommatidia.

Antennae.

The 11-jointed antennae are clubbed and somewhat longer than the head (fig. 1). All the joints are set with long hairs.

In *O. surinamensis* (fig. 1,a) the 9th joint is broader than long, the 10th joint is similar to the 9th but broader, whilst the 11th joint is narrower than the 10th but longer.

In *O. mercator* (fig. 1,b) the first two joints of the club (9th and 10th) are broader, in comparison with their length, than those of *O. surinamensis*, and their lateral margin outlines, in dorsal aspect, are somewhat angled, rather than flatly rounded as in *surinamensis*.

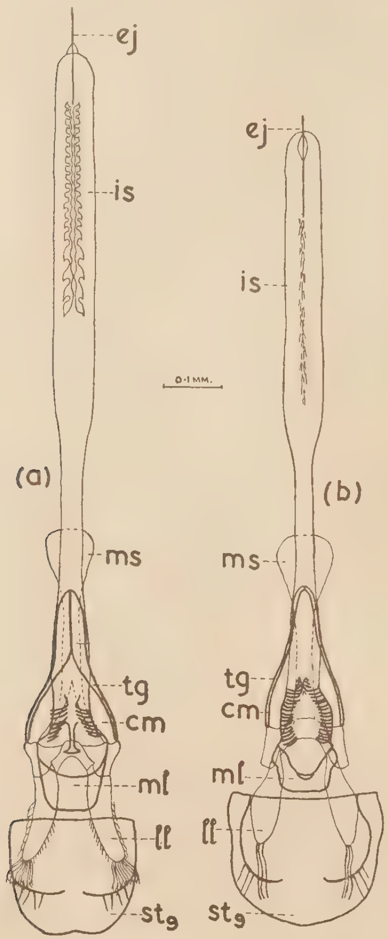


Fig. 2.—Male genitalia (ventral view) of (a) *O. surinamensis* and (b) *O. mercator*. ej, ejaculatory duct; is, internal sac; ms, median strut; tg, paired struts; cm, connecting membrane; ml, median lobe; ll, lateral lobe; st_9, ninth sternite.

Thorax.

The pronotum of *O. surinamensis* is slightly wider than the head at the temple, and the anterior margin is convex, the posterior margin straight. The sides are slightly convex, and each bears six teeth, of which the foremost and hindmost are more pronounced than those between. There are three ridges on the pronotum, the median one straight and the lateral ones convex, so that the furrows which lie between are also convex.

The pronotum of *O. mercator* is broader and stouter than that of *O. surinamensis*, and considerably wider than the head at the temple. It is more convex at the sides, but the furrows between the ridges are more parallel-sided.

There are no other differences of thoracic structure between the species.

Male genitalia.

There are obvious specific differences in the male genitalia (figs. 2–6). The aedeagus consists of a tegmen (ventral view, figs. 2 & 3), comprising paired struts (tg), basal piece (bp) and lateral lobes (ll), which forms a ring round the median lobe (ml), and is connected to it by a membrane. The lateral lobes, lying on the dorsal side of the median lobe, are dorsoventrally flattened (fig. 3). The setae on the outer sides of the lateral lobes of *O. mercator* are all short (fig. 3,b) whereas in *O. surinamensis* (fig. 3,a) they are all long; *surinamensis* also carries some shorter setae on the inner sides whereas in *mercator* these are confined to three or four very short setae towards the distal extremity.

In *O. surinamensis* the setae at the apex of the lobe are long and branched at the ends (fig. 3,a) and number about ten, whereas in *O. mercator* there are only three or four long setae at the apex of the lobe (fig. 3,b) and they are not branched but spatulate. At the proximal end of the lobe, on the inner side, there

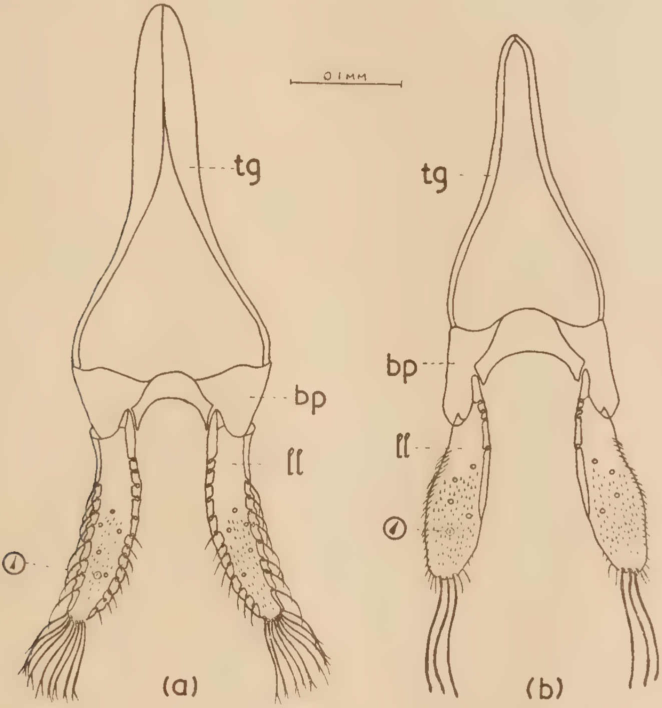


Fig. 3.—Male genitalia (ventral view) of (a) *O. surinamensis* and (b) *O. mercator*: tegmen and lateral lobes. bp, basal piece; other lettering as in fig. 2.

are several flask-shaped glands. The surface of the lobe is rough, being covered with small spines which are directed towards its base. There are also about five or six peg-like projections standing up from the surface. The small spines on the surface of the lobes of *O. mercator* are broader (fig. 3,b) than those of *O. surinamensis* (fig. 3,a). The difference in the shape of the lateral lobes in the two species is sufficiently great to allow identification of the species by this character (figs. 2 & 3). The basal piece (bp) of the tegmen lies on the dorsal side of the median lobe, and from the broad plate which bears the lateral lobes the two struts (tg) pass round the median lobe and join on the ventral side. The connecting membrane lies between these struts.

The median lobe (fig. 4) is dorsoventrally flattened, and bears a number of short stiff setae on the posterior part. In *O. mercator* these setae are confined to the sides (fig. 4,c). In front of this part is the median orifice (mo), through which the internal sac (is) is evaginated. The median orifice is partly surrounded by curved chitinous rods (ct), of which there are about eight on each side in *O. surinamensis* (fig. 4,b). These curved chitinous rods are shorter in *O. mercator*, and there are about sixteen on each side instead of eight (fig. 4,c). These rods support the hindermost part of the V-shaped median foramen (mf), through

which the ejaculatory duct (ej) passes. The internal sac, which is the broadened posterior part of the ejaculatory duct, is long, and has in *O. surinamensis* an elaborate saw-toothed structure within (fig. 4,a), into which the narrower part of the ejaculatory duct opens. The surface of the internal sac is covered with short spines arranged in diagonal rows. In *O. mercator* the internal sac has no definite saw-toothed structure inside it (fig. 4,d).

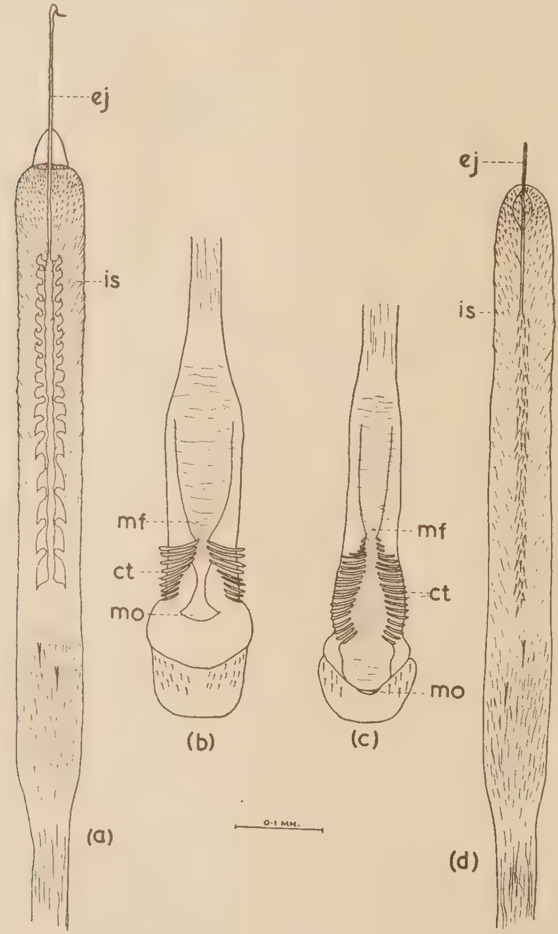


Fig. 4.—Male genitalia of (a), (b) *O. surinamensis* and (c), (d) *O. mercator*: internal sac and median lobe. mf, median foramen; ct, chitinous rods; mo, median orifice; other lettering as in fig. 2.

Attached to the dorsal surface of the median lobe is a median strut (fig. 2,ms) shaped like an inverted Y with a broadened base (fig. 5). The shape of this median strut is also characteristically distinct between the two species.

The tegmen is connected to the ninth abdominal sternite by a second membrane. Joined to this membrane by its forked end is a Y-shaped spiculum (fig. 6,sp) lying on the dorsal side of the aedeagus. The eighth sternite is divided

into two plates, each of which in *O. surinamensis* has a few fairly long setae and a number of very short ones on its edge. The long setae vary in number and length but there are never less than four on each lobe in *O. surinamensis* (fig. 6,a).

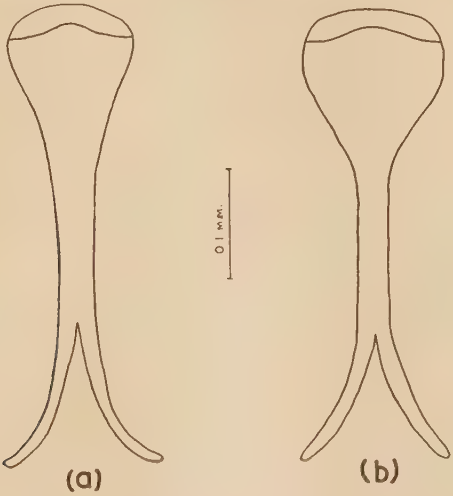


Fig. 5.—Median strut from male genitalia of (a) *O. surinamensis* and (b) *O. mercator*.

In *O. mercator* there are only three long setae with no short ones interspersed. They are placed near the outer edge, the one nearest to the edge being shorter than the other two.

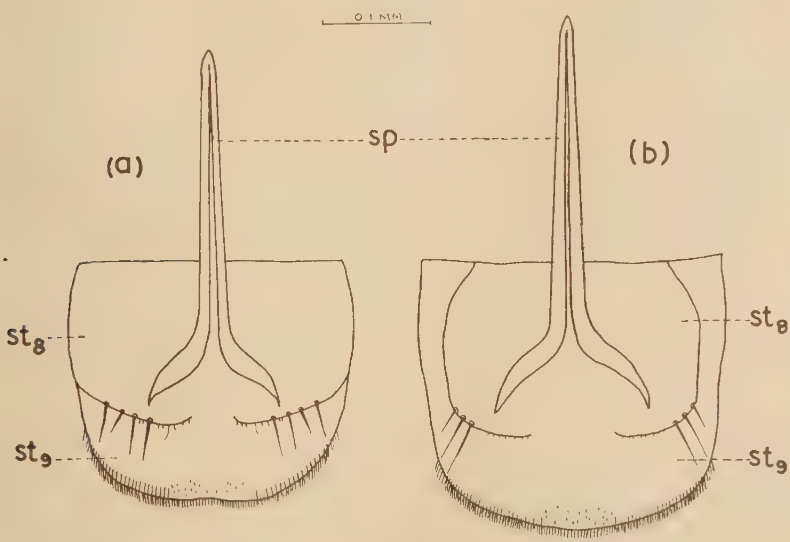


Fig. 6.—Male genitalia of (a) *O. surinamensis* and (b) *O. mercator*: abdominal sternites eight and nine. sp, spiculum; st_8, eighth sternite; st_9, ninth sternite.

To sum up, the features in the male genitalia which can be used to distinguish the two species are as follows:—

Character	Illustrated in figs.	*O. surinamensis*	*O. mercator*
Shape of lateral lobes	2, 3	(2,a; 3,a)	(2,b; 3,b)
Number of setae at end of lateral lobes	2, 3	(2,a; 3,a) about 10	(2,b; 3,b) 3–4
Number of chitinous rods in median lobe	2, 4	(2,a; 4,b) about 8	(2,b; 4,c) about 16
Structure of internal sac	2, 4	(2,a; 4,a)	(2,b; 4,d)
Shape of median strut	5	(5,a)	(5,b)
Setae of eighth abdominal sternite	2, 6	(2,a; 6,a) at least 4 long + some short ones	(2,b; 6,b) 3 long only

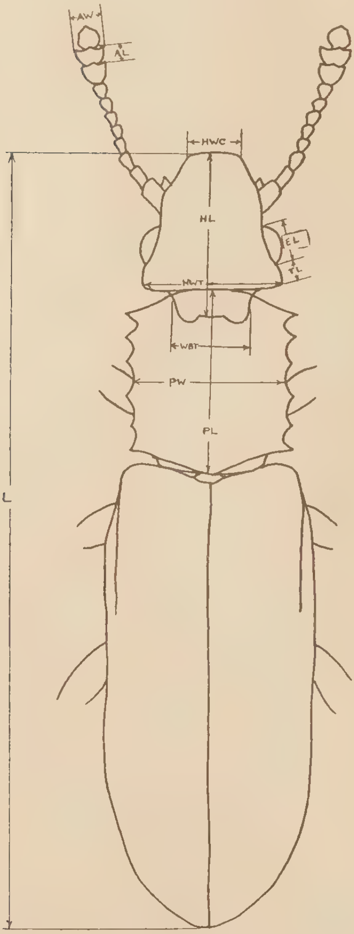


Fig. 7.—*O. surinamensis* (diagrammatic) showing measurements used in biometric examination. L, length of body; AW, width of 2nd joint of antennal club; AL, length of 2nd joint of antennal club; HWC, head width at clypeus; HWT, head width at temple; HL, head length; WBT, head width behind temple; PW, pronotum width; PL, pronotum length; EL, eye length; TL, temple length.

Female genitalia.

No specific differences have been found in the female genitalia.

Biometry.

A number of measurements of various parts (fig. 7) of the insects was made, using specimens collected in ships at British ports from produce loaded in various parts of the world, together with some specimens from stock cultures. The measurements were made on 133 beetles identified by the eye/temple ratio as *O. surinamensis* and 82 identified as *O. mercator*. The material of *O. surinamensis* was mainly from Australian, Burmese and Argentinian cereals, that of *O. mercator* from West African, Burmese and Argentinian oil-seed products. There was a considerable overlap of dimensions for the two groups so a number of ratios of the various measurements were computed. Of these, only one, the ratio of eye length to temple length originally used to distinguish the groups, does not overlap. Several others differ widely on average but overlap in range and are therefore not completely diagnostic. Since the eye length/temple length ratio corresponds with differences in the male genitalia it can be used to diagnose the species.

The most useful ratios are given in Table I, and the range of variation in certain measurements and ratios for both species are shown in fig. 8.

Breeding Experiment.

Single pairs of adults of either *O. surinamensis* or *O. mercator* identified as shown above, and mixed pairs of the two were placed in 3 in. by 1 in. specimen tubes on crushed groundnuts. The tubes were covered with muslin and kept at 27°C., relative humidity 70 per cent. After three to four weeks the adults were removed, so

TABLE I.

Measurement or ratio	*O. mercator* mean and range	*O. surinamensis* mean and range
Length (L) in arbitrary units	207·8 (185–243)	188·3 (162–214)
Eye length/temple length (EL/TL)	4·27 (3·0–5·5)	1·76 (1·25–2·25)
Head width at temple/head width at clypeus (HWT/HWC)	1·67 (1·48–1·83)	1·80 (1·61–2·03)
Head width at temple/pronotum width (HWT/PW)	0·77 (0·63–0·82)	0·86 (0·80–0·97)
Head width at temple/width behind temple (HWT/WBT)	1·29 (1·12–1·36)	1·40 (1·31–1·62)
Head length/pronotum width (HL/PW) . .	0·96 (0·88–1·05)	1·07 (0·97–1·19)
Width/length of 2nd joint of antennal club (AW/AL)	1·66 (1·20–2·14)	1·33 (1·10–1·63)

that the offspring should not be confused with the parents, and the larvae and pupae were counted. No offspring was obtained from the cross in either direction but all the cultures of each of the two pure species produced flourishing

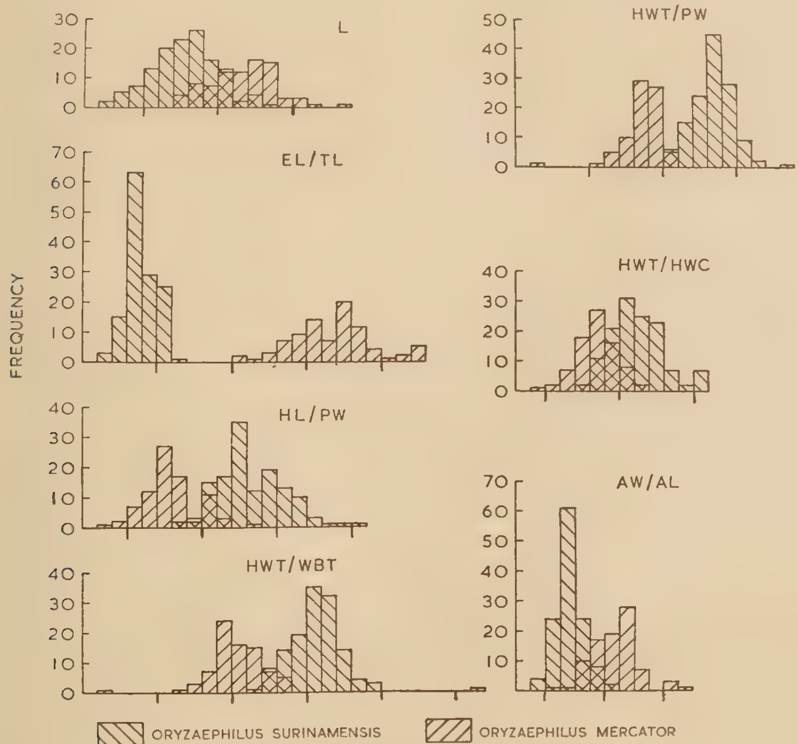


Fig. 8.—Histograms showing distribution of measurements and ratios given in Table I. For lettering, see fig. 7.

populations. No dissection of the females was made so it is not known if inter-specific pairing was attempted or achieved.

Conclusion.

The existence of a reliable distinguishing feature in the eye character, and of several good differences in the male genitalia, together with the failure of crossing between the species establishes that *O. mercator* is a good species and not merely a variety of *O. surinamensis*.

Summary.

The object of the work described in this paper was to compare adults of *Oryzaephilus surinamensis* (L.) and *O. mercator* (Fauv.) by morphological and biometric methods with a view to determining the status of the latter as either a variety of *O. surinamensis* or as a separate species.

There are some marked and constant differences between the two insects in the structure of the male genitalia. These are listed.

The analysis of the biometric results shows a clear-cut difference between the two insects in the ratio of eye length to temple length. All the other ratios considered overlap, although the means may be widely different. Some of these ratios are illustrated by histograms.

A cross-breeding experiment gave no offspring from the mixed pairs.

It is concluded that *O. mercator* is a good species which can be recognised morphologically.

Acknowledgements.

My thanks are due to Mr. R. W. Howe of the Pest Infestation Laboratory, Department of Scientific and Industrial Research, Slough, for his kind assistance in the preparation of the manuscript and for many helpful suggestions. The work was done under the supervision of Dr. W. F. Jepson at the Imperial College Field Station, Silwood Park.

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THE MATING BEHAVIOUR OF FEMALES OF *GLOSSINA PALPALIS* (R.-D.) IN CAPTIVITY.

By A. M. JORDAN, Ph.D.

Research Entomologist, The West African Institute for Trypanosomiasis Research, Kaduna, N. Nigeria.

The act of mating in tsetse flies has been described by a number of authors (Mellanby, 1936; Vanderplank, 1948; Squire, 1951; and Nash, 1955); it is also known that the female of *Glossina palpalis* (R.-D.) usually becomes fertilised when young (Mellanby, 1936; Nash, 1955). There is, however, little information available concerning the readiness of female flies to mate at different ages, although it is generally assumed that the teneral stage is the mating phase *par excellence* (Squire, 1952). Squire (1952) also recorded isolated instances of young female flies re-mating on a number of occasions but gave no details of the proportion of flies which behaved in that manner. The same author predicted a resurgence in mating desire later in the life of at least some females but evidence for this is scanty (Nash, 1955).

The Entomology Section of this Institute breeds large numbers of *G. palpalis* but there are still gaps in our knowledge of the mating behaviour of the female which the present investigation was designed to fill.

Methods.

In the fly-breeding room newly emerged flies were collected daily between 8 a.m. and 9 a.m. As shown by Nash (1955), about 75 per cent. of such flies are 14–24 hours old, but following the practice of Nash (1955) and, it is thought, of Mellanby (1936), the age of these flies was taken to be one day.

The flies were mated in mating cages, 7 × 6 × 6 inches in size, which consisted of a wooden framework and base, with a glass top and mosquito-netting sides. All flies were given the opportunity to feed on goat blood for half an hour before being placed in a mating cage. Except when otherwise stated, six females were present in each cage, the number of males present being always double the number of females. Throughout the experiments the mating cages were placed on the same bench in the fly room, in front of a window. The climate of the fly room was controlled, the temperature varying between extremes of 76° and 81°F. and the relative humidity between 70 and 85 per cent.

The six female flies in each mating cage were readily identifiable, each being marked on the prothorax with a single spot of a different coloured oil paint; they were kept under observation for the first five hours after males were added to the mating cage. Records were made of those that paired immediately after the addition of males, followed by further observations of those pairing at 15-minute intervals throughout the five hours of the experiment. Nash (1955) showed that copulations are most numerous shortly after the sexes are put together and that the number then decreases, becoming only a quarter as numerous six hours later. His figures, however, were not derived from observations of individual females but from the total number of pairs observed in the mating cage at various intervals during the first 24 hours. As will be shown later, some pairs are maintained for several hours, so it seems likely that more than 75 per cent. of the females which would have mated in 24 hours would have paired within the first 6 hours. The observational period of five hours used in the following experiments therefore

probably included up to 75 per cent. of the females which would have mated during the course of 24 hours.

Throughout all the experiments virgin males, 7 days old, were used in the mating cages. It has been shown that males of *G. palpalis* of this age are both more potent (Mellanby, 1936) and more virile (Nash, 1955) than younger males.

It was shown by Mellanby (1936) and confirmed by Nash (1955) that sperm does not pass until just before the pairs separate of their own volition. Both these authors also noted the occurrence of apparently normal pairs which persisted for a few minutes but which then separated; Mellanby found that none of these females was fertilised. In the present series of experiments, no female was assumed to have mated successfully unless at least two *consecutive* observations of mating were made, indicating that copulation had lasted for at least 15 minutes. Spermathecal examinations of a sample of such females showed that they were all impregnated; none of these females, however, were found to have both vesicles completely full. In experiments carried out by Mellanby (1937), females of *G. palpalis* were not taken as fertilised until they had mated for at least half an hour.

The Duration of Mating.

A number of workers have referred, in passing, to the duration of mating in tsetse flies but no exact information on this subject has been found. Mellanby (1936) stated that "copulation lasts for from half an hour to two hours in the tsetse", Squire (1951) that it lasts "sometimes for several hours" and Nash (1955) that it is "usually a matter of one or two hours". During the present investigations the duration of mating in virgin females of *G. palpalis* of different ages was determined somewhat more accurately, although for the following reasons the figures obtained were all minimal. Firstly, since there were 15 minutes between observations, any one pairing could have been up to half an hour longer than recorded. Secondly, a small number of flies were still pairing at the end of the five-hour period of observations and would have continued to do so for an unknown time; to compensate, such flies were always recorded as having paired for one additional quarter of an hour, but such degree of compensation was, of course, quite arbitrary. The results which were obtained from groups of virgin females 1 to 10 days of age are shown in Table I. The Table shows that flies of these ages can be divided into three groups. The first group, of flies 1–3 days old, mated, on the average, for about two hours; it is not known what

TABLE I.

The duration of mating in virgin females of *G. palpalis*.

Age of females (days)	Total matings	Mean duration of mating (minutes)
1	103	109
2	66	130
3	210	106
4	59	73
5	74	76
6	53	70
7	38	75
8	40	79
9	42	76
10	32	54

For the reasons given in the text, the durations given in the last column of the Table are minimal figures.

significance, if any, can be attached to the performance of the 2-day-old flies. Flies 4–9 days old mated for a markedly shorter average period than the flies 1–3 days old, but there was little difference between each of these age-groups and the mean length of each mating was about 75 minutes. The thirty-two 10-day-old flies formed the third group and only mated for an average of somewhat less than one hour. There is, therefore, evidence of a decreasing mean length of the initial copulations by virgin females, with increasing age of the flies.

The maximum period of copulation observed was 7½ hours; the female was a 3-day-old fly which had already mated for 1¼ hours when two days old.

The Age at which Females will Mate.

Mellanby (1936), working with *G. palpalis fuscipes* Newst. in Uganda, found that females 5–8 days of age were more attractive than flies less than five or more than eight days of age. Squire (1952) and Nash (1955), working in West Africa with *G. palpalis palpalis*, came to a different conclusion; they found that the youngest females were most eager to mate. Squire (1952) concluded that the teneral stage is the mating phase *par excellence*; he found that the absence of mating scars was practically confined to such flies. He estimated that the teneral stage ends about seven days after emergence. Nash (1955) carried out experiments which suggested that females 6–8 days old were less attractive to males than others 1–5 days old. These experiments suggested that those 3 days old were possibly the most attractive. As mentioned above, Nash's figures were not obtained from observations of individual females but from the total number of pairs observed in the mating cages when using different batches of females of known age. He did not quote these results as his main object was to determine in which age-group maximum fertilisation, and not mating, occurred and this he determined by spermathecal examination. He found from such examinations that the fertilisation rate was highest amongst 3-day-old flies; flies 1–5 days old were more readily fertilised than flies 6–10 days old. It was decided to try to find out whether this picture was due to a difference in the readiness of the various groups of flies to mate, or whether some age-groups of flies were more easily impregnated than others. It has already been shown (p. 36) that the duration of mating decreases with increasing age of the females and this may be sufficient to explain the lower number of females which became fertilised in the older age-groups.

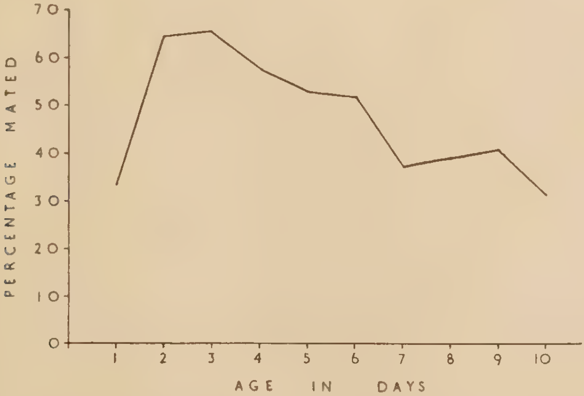

Fig. 1.—The percentage of virgin females of *G. palpalis* of different ages (102 females of each age) which mated when left for 5 hours with twice as many 7-day-old virgin males.

An experiment was carried out in which batches of females of each age from 1 to 10 days old were caged with twice their number of 7-day-old males. As over 1,000 female flies were used in this experiment it was considered too extravagant of the Institute's breeding stock to dissect the flies to check the number fertilised against the number known to have mated. The percentage of matings which occurred are shown graphically in fig. 1.

The figure suggests that mating is relatively infrequent with 1-day-old females, maximal with females 2 and 3 days old, and thence decreases as the age of the female increases. The performance of 1-day-old flies was significantly worse than that of 2-day-old flies (χ^2_c = 18·850; $P<0{\cdot}001$) but, apart from a just significant drop in the performance of 7-day-old flies, compared with 6-day-old flies (χ^2_c = 3·888; P = 0·05), the difference in performance of any two adjacent age-groups is not significant. It is not known, and is probably not important as far as natural populations are concerned, what the maximum age is at which a virgin female will mate for the first time. It is of interest to note that fifteen 30-day-old virgin females failed to mate when thirty 7-day-old males were placed with them. Buxton & Lewis (1934), working with *G. tachinoides* Westw., found that some virgin females, mated on the 45th day, eventually produced puparia.

The results shown in fig. 1 can be compared with those obtained by Nash (1955) for the number of females of *G. palpalis* found to be fertilised after a period of 24 hours with males. He dissected 90 females of each age from 1 to 10 days old, and found a decline in the number fertilised from the third day onwards. The 1-day-old flies (74·4% fertilised) showed a better performance than the 2-day-old flies (64·4% fertilised) but not so good as the 3-day-old flies (84·4% fertilised). The general pattern of a decline in mating potential, leading to a lower percentage of fertilisation as the flies age, is apparent from both sets of figures. Nash's larger figures were due to the sexes being together for 24 hours against only five hours in the present mating experiments. The performance of flies 1 and 2 days old does not conform in the two series of experiments. Whereas Nash (1955) found that 74·4 per cent. of 1-day-old flies became fertilised after 24 hours, only 33·3 per cent. of these flies were found to mate in the five hours of the present experiment. The difference could be explained if very young females are not prepared to mate: some of these "1-day-old" flies were really only a few hours old (see p. 35). Such very young females would have had time to become sufficiently old to mate during the 24 hours of Nash's experimental mating period, but not in the present experimental mating period which lasted for only five hours. No explanation can be given for the better performance of 2-day-old flies in the present experiments. These, however, are minor discrepancies; the present experiments confirm the findings of Nash (1955) and explain that the reason he obtained maximal fertilisation on the third day of female life and lower fertilisation thereafter, was because the females are most willing to mate when 3 days old and progressively less willing as they become older.

The Frequency of Re-mating amongst Females.

It has been generally assumed that one mating suffices to supply the female tsetse with sperm for the whole of her life; Mellanby (1936) dissected a once-mated fly 200 days old and recorded the presence of living spermatozoa in the spermathecae. However, Squire (1952) suggested, from observations of a laboratory-maintained stock of *G. palpalis*, that, during the teneral stage, females are "repeatedly and vigorously mated". He quoted two instances, one in which a laboratory-bred female was twice mated on the first day and twice again on the third day, with a total period in copulation of two and a quarter hours; in a second instance, a female mated three times in the first four days of adult life. If occurrences such as these are common in nature, any means of eradication

of tsetse based on the release of sterilised male flies, as has been suggested, would prove impracticable, as the chance of a female fly eventually mating with an unsterilised male would obviously be much increased. The technique of releasing sterilised flies into a natural population has been successfully used in eradicating the screw-worm fly, *Callitroga hominivorax* (Coq.), from the island of Curaçao (Baumhover & others, 1955) but the females of this species mate only once.

Laboratory experiments were carried out to determine the proportion of young females of *G. palpalis* which behave in the manner described by Squire (1952). In the first experiment, females of *G. palpalis* were given the opportunity to mate for five hours every day for the first six days of their life; the flies were thus with males for a total of 30 hours. A fresh batch of 7-day-old males was used on each day of the experiment. Table II (Experiment I) shows the number of females which mated once, twice, thrice, etc., during the six days of the experiment; the figures given are for those females (103 in number) which lived throughout the period and not for the initial number (263) or the number of flies alive on each day (see Table IV). If less than six females remained alive in a mating cage appropriately fewer males were used on that and succeeding days in order to maintain the 2 : 1 ratio of males to females. From Table II it can be seen that 99 out of 103 females (96·1%) mated and that, of the 99 mated flies, 74 (74·7%) mated on at least two occasions. Amongst the 99 mated flies the average number of matings per female was 2·2.

TABLE II.

The frequency of mating among young females of *G. palpalis* of two age-groups.

Number of matings	Number of females	
	Experiment I (Ages 1–6 days)	Experiment II (Ages 5–10 days)
0	4	29
1	25	53
2	43	14
3	21	5
4	6	2
5	4	0
6	0	0
Total	**103**	**103**

In a second experiment (Experiment II of Table II), older females, 5–10 days of age, were given daily opportunities to mate. With flies of these age-groups 74 out of 103 females (71·8%) mated and 21 of the mated flies (28·4%) mated on at least two occasions. The average number of matings amongst the mated flies was 1·4.

As expected, from previous results given in fig. 1, the proportion of females which mated in the age-groups 5–10 days old was less than in the age-groups 1–6 days old. Similarly, the occurrence of re-mating was more frequent among the younger flies, but even amongst the older flies re-mating was not unusual. The possible significance of these results, relative to the situation in nature, is discussed on p. 42.

From Mellanby's (1936) results, already quoted, it is known that females can store active spermatozoa for up to 200 days. Thus, if a female fly is to remain productive at as late an age as this, re-mating later in life does not appear

imperative. On the other hand, Squire (1952) stated that older females are mated on occasions and he thought this necessary as 5 per cent. of his oldest age-group, although showing mating scars, had empty spermathecae. He suggested that there are post-teneral "safe periods" during which the female will allow mating, such periods being when the superior claspers of the male could do no damage to a developing larva within the female. Squire thought these periods would occur when a third-stage larva was present in the uterus (when the polypneustic lobes would act as a protection from the claspers), and between larvipositions when the uterus is empty. In three experiments with *G. palpalis* carried out by Nash (1955), 16 females of 65–71 days of age failed to re-mate when placed with twenty-one 7-day-old males; of 20 females, at least 73 days old, 4 re-mated for periods up to one hour; and of 13 females, about 123 days old, none re-mated. Nash recorded that the females were not willing to mate, and the copulation of any pairs, except for the four in the second experiment, was of short duration.

An experiment was carried out to determine the proportion of older females of *G. palpalis* prepared to re-mate. Females were mated at 3 days old and were then given opportunities to re-mate at weekly intervals for the rest of their lives. The results are given in Table III.

TABLE III.

The amount of re-mating by post-teneral females of *G. palpalis*.

Age of females (days)	Number of females	Number of females which re-mated
10	146	1
17	104	1
24	81	1
31	63	0
38	48	0
45	38	0
52	29	0
59	23	0
66	17	0
73	12	0
80	5	0
87	4	1
94	3	0
101	2	0
108	1	0
115	1	0
122	1	0

The figures given in Table III do not support Squire's (1952) hypothesis for the existence of successive "safe periods" during which older females would be prepared to re-mate. The number of females alive in the oldest age-groups was low so it cannot be said that very old females are not prepared to re-mate but, on this evidence, it seems unlikely. The one 87-day-old female which did re-mate was in an extremely weak condition and apparently could not resist the attentions of the male; it remained in copulation for $2\frac{1}{2}$ hours and died during the following night. Many of the females which were given opportunities to re-mate in this experiment were attractive to males and struggling pairs with copulations of short duration were common, but, as shown in Table III, only four flies were observed pairing for at least two consecutive observations. The usual reaction of an old female to a male attempting to pair was to repel him by

vigorous movements of the wings. These tentative copulations were most common immediately after the addition of males to the mating cages. Nash (1955) also noticed these brief copulations with old females of *G. palpalis*.

The Effect of Mating on the Capacity for further Mating.

From figures given in two of the preceding sections it can be shown that a once-mated female was less willing to mate than a virgin female of the same age. From fig. 1 and Table IV it can be seen that 31·4 per cent. (32 out of 102) *virgin* 10-day-old flies mated whereas, from Table III, only 1 out of 146 (0·69%) *once-mated* 10-day-old flies mated again. The difference is highly significant ($\chi^2_c = 46{\cdot}396$; $P < 0{\cdot}001$).

The same phenomenon can be demonstrated from an examination of the figures obtained in the experiments on the frequency of mating (from which Table II is derived) in which females of *G. palpalis* were given opportunities to mate and re-mate during days 1 to 6 (Experiment I) and days 5 to 10 (Experiment II) of their lives; these figures can be expressed as the proportion of flies of each age which mated, or re-mated. All flies alive on each day have been included and not just those alive at the end of the experimental period as in the compilation of Table II. The results are given in Table IV in which comparable figures for virgin flies are also given.

TABLE IV.

The mating potential of previously mated females of *G. palpalis*.

Age of females (days)	Experiment I (Females mated days 1–6)			Experiment II (Females mated days 5–10)			Virgin females that mated at age shown (from fig. 1) (%)
	Females alive	Females mated	% mated	Females alive	Females mated	% mated	
1	263	101	38·4*	—	—	—	33·3
2	233	98	42·1	—	—	—	64·7
3	169	57	33·7	—	—	—	65·7
4	141	42	29·8	—	—	—	57·8
5	117	17	14·5	144	73	50·7*	52·9
6	103	13	12·6	137	27	19·7	52·0
7	—	—	—	128	8	6·2	37·3
8	—	—	—	122	7	5·7	39·2
9	—	—	—	113	4	3·5	41·2
10	—	—	—	103	3	2·9	31·4

* Being the first day of the experiment these figures refer to virgin females.

Ignoring the first figures in Experiment I and Experiment II, which refer to virgin flies, it is obvious from Table IV that the mating potential of the previously mated flies was much less than that of the virgin flies of equivalent age shown in the last column. The difference is significant with females of all ages (χ^2_c = 10·827 and $P < 0{\cdot}001$ in all cases).

This decrease in capacity for further copulation in previously mated females of *G. palpalis* was further demonstrated in an experiment in which females were first given the opportunity to mate when 1 day old; the mated flies were then separated from those which had failed to mate and kept without males until 3 days old. The mated females were then placed in mating cages with males. Sixty females were treated in this way and 19 (31·7%) of them mated. It will be seen from fig. 1 that 65·7 per cent. of virgin females of this age mated. The

difference between the proportions of 3-day-old females which mated when virgin, and when once-mated, is significant ($\chi^2_c = 16{\cdot}216$, $P < 0{\cdot}001$).

The difference in performance of virgin and previously mated flies may be due to a decrease in desire for mating by the females or to a loss of attractiveness to the male. It seems that the former is the most likely explanation as " attacks " by males on apparently unwilling females were often noted, especially immediately after the addition of males to the mating cages.

Discussion.

The results of the above series of experiments have confirmed that mating by females of *G. palpalis* is almost confined to early life; after the third day it can be said that the older the virgin, the less likely she is to mate. There is no reason to doubt that the same occurs in nature, because Squire (1951) found that females without mating scars were nearly always very young. The duration of copulation is longest with virgin flies 1–3 days old, considerably less with flies 4–9 days old, with possibly a still further decline in 10-day and older females.

It has been established in the laboratory that many young females of *G. palpalis* are prepared to re-mate, but there is no evidence of extensive re-mating among older females of 10 or more days of age. In nature, teneral females are considerably outnumbered by older, and therefore potent, males; hence, conditions for numerous matings of each young female would seem to be more favourable in nature than in the laboratory experiments.

Frequent mating of each female, however, may not necessarily occur under natural conditions. For instance, Gillies (1956), working on *Anopheles gambiae* Giles, found that the male secretes a plug of albumen-like material in the oviduct of the female, which persists for about 24 hours after mating; double plugs were sometimes found in laboratory-bred mosquitos, indicating fertilisation by more than one male, but only single plugs were found in wild-caught females. This would appear to suggest that multiple mating takes place only in the confined space of a cage in the laboratory, and that the behaviour of a once-mated female of *A. gambiae* is such that she secludes herself from further attentions by males. Although no mating plugs have been found in *G. palpalis*, similar behaviour might occur, and it could be that the decrease in mating desire of previously mated females, demonstrated in the present laboratory experiments, is an indication of this. However, in West Africa the proportion of females in a catch of wild flies is rarely very much lower than that of males (Nash, 1948; Nash & Page, 1953), which suggests that a once-mated female does not become fugitive in her habits.

Having briefly reviewed the evidence, it would appear that a considerable proportion of young females are likely to mate in nature on a number of occasions, but that the desire for mating is extinguished much sooner in life in mated females than it is in virgin females.

Summary.

Experiments were carried out in the laboratory with individually marked females of *Glossina palpalis* (R.-D.); various aspects of their mating behaviour, when placed with virgin 7-day-old males, were studied.

Using virgins, females 1–3 days old mated for an average period of about two hours, females 4–9 days old for about 75 minutes, and 10-day-old females for somewhat less than one hour.

Using virgins, mating was found to be relatively infrequent in 1-day-old females, maximal in females 2 and 3 days old and thereafter decreased as the age of the females increased.

Females up to 10 days of age were found to be willing to mate on a number of

occasions; re-mating was more frequent among the younger flies. The number of older females of *G. palpalis* which are prepared to re-mate is very small.

Previously mated females of *G. palpalis* were shown to be less willing to mate than virgin females of the same age. It seems that this is due to a decrease in desire for mating by the females rather than a loss of attractiveness to males.

The implication of these laboratory findings, in relation to fly behaviour in the field, is discussed. It is suggested that a considerable proportion of young females of *G. palpalis* is prepared to re-mate in nature, on a number of occasions, but that the desire for mating is extinguished much sooner in life in mated females than it is in virgin females.

Acknowledgements.

I am indebted to Dr. T. A. M. Nash, Director, West African Institute for Trypanosomiasis Research, for permission to publish this paper, and also for much helpful discussion during both the course of the experimental work and the preparation of the manuscript. Mallam H. M. Yesufu, Technical Assistant in charge of the fly-breeding room, arranged for the mating of the flies used during the experiments, and carried out most competently the routine observations on the flies in the mating cages.

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AN IMPROVED TECHNIQUE FOR PERMANENT MOUNTS OF SMALL INSECTS AND NEMATODES.

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In a previous publication (Colless, 1951), a method was given for preparing permanent mounts of mosquito larvae, etc., using a phenol-balsam mounting medium (Canada balsam dissolved in liquid phenol). The technique described had been found useful in practice, but had certain disadvantages, and it seemed at that time likely that more satisfactory methods would soon be developed. using some of the new synthetic media, such as polyvinyl alcohol. Such, however, has not been the case. Mounts made with polyvinyl alcohol became badly flattened due to the shrinkage of the medium, and, in any case, mosquito larvae, at least, show a strong tendency to shrivel in this medium—I have tested three proprietary formulations, all with poor results. Other media, such as " Sira ", of the balsam-substitute type, may possess improved colour or refractive index. but these require lengthy and very careful handling of the specimen before it is brought into the medium. Obviously, what is required is a method which combines the ease and rapidity of Berlese-type or polyvinyl alcohol techniques, with the permanence of Canada balsam.

A near approach to this optimum, for certain types of specimen, has recently been announced by Grenier, Adam & Hamon (1956). Their " Baume à chaud " method involves placing the specimen direct into melted balsam, and is extremely rapid and useful. It does, however, suffer from certain disadvantages—delicate specimens sometimes shrivel, particularly if cleared or macerated, and it is difficult to arrange the specimen in a given position. For these reasons, it is felt that the phenol-balsam method is still the best available, using a modified technique which has been developed over the past five years.

The technique originally described (Colless, *op. cit.*) suffered from two major defects. Firstly, balsam and phenol appear to form a loose compound, rather than a true solution, and hence the mounts take a long time to dry. Secondly. the medium, once prepared, does not keep well; it darkens with age, and has to be prepared afresh at least once a month. The first disadvantage is easily overcome by placing the specimen in a small drop of the medium, and, without covering, drying in the oven overnight. When dry, a little ordinary xylol-balsam is added, and the cover slip placed in position. This also allows very careful arrangement of the specimen, since no movement can occur when placing the cover slip in position.

To overcome the second disadvantage, it would clearly be preferable to prepare fresh medium on each occasion. This can, in fact, be quite simply done. by placing the specimen on the slide in a drop of pure phenol and *then adding dry powdered balsam*. The latter dissolves rapidly, but allows a very useful gradual transition, from phenol alone to phenol-balsam. This tends to counteract shrivelling in quite delicate specimens.

A further feature of the technique originally described was the use of strong chloral hydrate as a preliminary clearing agent, and further notes on its use are given below. The concentration recommended (see below) is simply that used in Gater's modification of the Berlese mounting medium, and could probably be varied considerably. It is an excellent clearing agent, though its action is greatest with live, or newly killed, specimens. With mosquito larvae, for instance, live

specimens dropped into the chloral hydrate solution become perfectly cleared in less than two hours—there is apparently a macerating action, since such specimens appear to consist of little more than a larval skin. However, with specimens which have been preserved for some time, the clearing action is little, if at all, better than that produced by the phenol bath, through which the specimens must in any case pass.

Full details of these clearing and mounting techniques are given in the schedules below.

Clearing.

A. In chloral hydrate solution.

This method is for live, or freshly killed, specimens, where a very transparent mount is required.

1. The specimen is placed in strong chloral hydrate solution (80 grammes in 20 cc. of 30% acetic acid) and left until cleared (about two hours, but may be safely left until required). Living specimens are preferable, since they will usually eject most, if not all, of their gut contents, and give a mount in which dorsal and ventral details are equally visible. At this stage it is sometimes useful, though not always essential, to nick the cuticle in several places, using fine needles.

2. The specimen is washed in 70–90 per cent. alcohol for about 10 minutes. This is not essential, but it avoids cumulative contamination of the next bath. For this and subsequent transfers, a small wire loop should be used.

3. The specimen is then transferred to liquid phenol (prepared by allowing crystals to liquefy at room temperature, or by warming if necessary). Specimens may be left in this bath until required.

B. In phenol.

This is an alternative to *A*, above, for preserved specimens, or where extreme transparency is not required. Fresh specimens should be killed in *warm* water or 70–90 per cent. alcohol, so that their body contents remain fairly plastic; otherwise they may be disfigured by bursting during step 2, below.

1. The specimen is placed in 70–90 per cent. alcohol, and, using fine needles, several nicks in the cuticle are made.

2. The specimen is then transferred to liquid phenol until cleared. Specimens may be left in this bath until required.

Mounting in Phenol-balsam.

1. Using a pipette, the specimen is transferred with a drop of phenol to the slide, about 0·03–0·05 cc. being a suitable size for the drop.

2. Any necessary dissections, arrangement, etc., are then performed.

3. A small amount of dry, powdered Canada balsam is sprinkled over the drop of phenol. The amount to be added can only be learnt by experience, but, as a rough guide, about 20 mg. balsam are required for a drop of 0·03 cc.; this is about five times as much as is lifted on a wire loop of 0·1-in. diameter. The amount of balsam added, and the size of the drop, may be varied according to the size and the delicacy of the specimen. Very delicate objects require a maximum of phenol and a minimum of balsam (just enough to give support when dried).

4. The arrangement of the specimen should be checked, and the preparation dried in the oven at about 110°F. overnight. Incomplete drying allows retention of a little phenol and thus enhances the refractive index of the medium, but it also slows the final drying of the mount.

5. A little xylol-balsam is added, and a cover slip placed in position.

6. The preparation is dried in the oven in the usual way.

Notes.

The above techniques were originally developed for mounting mosquito larvae, but have been found applicable to a wide range of small Arthropoda; for example, I have used them successfully with, *inter alia*, adult mosquitos and other small Diptera, dragonfly larvae, small caterpillars, Collembola (SMINTHURIDAE, but not ENTOMOBRYIDAE), fleas, ticks, and parasitoid mites; it is, of course, not suggested that other techniques may not give better results in certain cases. In certain groups, *e.g.*, the Ceratopogonid midges, great care must be taken not to add too much balsam initially; otherwise, the antennae, legs, etc., may collapse.

These methods have also been found very useful for preparing balsam mounts of certain nematodes, and have been tested successfully with adults of *Ancylostoma caninum*, *Toxocara cati*, and *Ascaris lumbricoides*. Presumably they may be applied to a much wider range of helminths. The chloral hydrate clearing bath alone is a very useful medium for temporary mounts, even with long-preserved specimens.

A further point worth noting is that the same, or a similar, mounting technique may be possible, using substances other than Canada balsam, and perhaps, solvents other than phenol; that is to say, that the technique of adding the solid medium to a specimen in a drop of clearing agent-solvent may be capable of considerable development and improvement.

Summary.

An improved technique is described for the preparation of permanent mounts of small Arthropoda and Nematoda, using a phenol-balsam mounting medium; a method is also described for clearing live, or freshly killed, specimens in strong chloral hydrate solution. The essential feature of the mounting method is the transfer of the specimen to a slide, in a drop of phenol, to which dry, powdered balsam is added and allowed to dissolve *in situ*. The mount is then dried and later covered in the usual fashion.

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BIOLOGICAL NOTES ON THE TOBACCO CRICKET, *BRACHYTRUPES MEMBRANACEUS* (DRU.) (ORTHOPT., GRYLLIDAE), IN SOUTHERN RHODESIA.

By W. W. Büttiker * and G. H. Bünzli *

(Plate I.)

The species of the genus *Brachytrupes* are mainly confined to the tropical and sub-tropical belt of Asia and Africa. The most common species in South and East Asia is the blackish-brown *B. portentosus* (Licht.) (syn. *achatinus* (Stoll)) whilst, in Africa, the similarly large *B. membranaceus* (Dru.) is recorded from Kenya, Tanganyika, Mozambique, Northern and Southern Rhodesia and the northern parts of the Transvaal. Results of field investigations will be found in two previous papers, dealing mainly with the chemical and biological control of this last-mentioned Gryllid (Bünzli & Büttiker, 1955, 1956).

The biology of the Asiatic species, *B. portentosus*, seems to be very similar to that of *B. membranaceus* according to Ghosh (1912) and Kalshoven (1951), particularly in respect of nocturnal feeding habits, type of food, and burrow system. Furthermore, both species have only one generation a year. Considerable damage by *B. portentosus* has been reported from India and Indonesia to cassava, chilli, kapok, coffee, tea, tobacco and *Hevea* (Dammerman, 1929). The Australian cricket, *Acheta* (= *Gryllulus*) *commodus* (Wlk.), was investigated by Browning (1954), who gives ecological data referring particularly to feeding habits, propagation, life-cycle and the burrow system.

Status and Incidence of *B. membranaceus* in S. Rhodesia.

In Southern Rhodesia, *B. membranaceus* is a pest of tobacco and maize, attacking the young seedlings in November–December. During the period of investigations, 1949–52, an indication of its importance as a pest was obtained from an analysis of 447 replies to a general entomological questionnaire sent to 2,400 tobacco farmers. These replies showed that the heaviest attacks were experienced in the South Salisbury and Trelawney–Darwendale districts, and the lightest in the Umvukwes, the areas most favoured being those in which the soil is of a light type, of granitic origin.

The Egg.

In shape, the egg is elongated and cylindrical with rounded ends (Pl. I, fig. 1). The length of the newly laid ovum varies between 3 and 4 mm. (average 3·1 mm.) and the width ranges between $1\frac{1}{3}$ and $1\frac{1}{2}$ mm. When freshly laid, the colour is white, turning to dark brown after a few hours. As they mature, the eggs swell up considerably and reach a length of approximately 5 to 6 mm.

From January 1950 onwards, females were kept in sand-filled cages (Pl. I, fig. 3) or large boxes, either singly or in pairs, in the hope that eggs would be obtained in the burrows. Eventually oviposition took place but, unfortunately, only in a few instances. One female collected and caged had produced 87 eggs by 24.iii.50. Another female dug out on 1.iii.50 had deposited 25 eggs by 10.iii.50. A third female caught on 30.i.50 had laid 27 eggs by 13.ii.50. These

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eggs were kept in the incubator at 25°C. and one hatched on 10.iii.50 and another one on 11.iii.50.

The total number of eggs laid by a female may well be over 300.* Dissection of the ovaries of 22 females showed that the number of eggs per female varied from 50 to 332 with an average of 216.

According to observations made in the field and insectary, the eggs are laid in February and March. Since incubation takes about 30 days, young crickets can be expected to be present in the fields at the earliest in March and April. Only twice did we succeed in findings eggs in the field; on 2nd April in a deserted cricket hole, close to the main chamber some 65 cm. below surface level, and on another occasion batches of eggs, close together, at the bottom of the main chamber.

The Nymph.

The first-instar nymph measures between 4 and 6 mm. upon emergence. Specimens reared in the humidity-controlled incubator at between 70 and 80 per cent. R.H. needed approximately 12 days at 22°C. to reach the second instar.

After two or three days the young crickets abandon the old nest system and start to excavate their own individual burrows, and at the end of March and beginning of April active first-stage nymphs are present in the new burrows. From the beginning of May the results of their foraging are kept in the main bottom chamber. These consist of cut fresh vegetation (weeds, regrowth of trees, etc.) and also of dead, wind-blown leaves of woody plants, scraps of tobacco plants including seed capsules, together with shorth lengths of woody débris.

In the bush veld in the Salisbury-South district the first young nymphs, 8 mm. to 10 mm. in length, were unearthed on 3rd April from a depth of 2·5 to 5 cm. Their presence in the soil was revealed by small, open holes.

More advanced stages of juvenile crickets were discovered on 29th June on a farm, north of Macheke, in a tobacco field in which the stalks had not yet been pulled. The still rather shallow burrows were scattered over ridges and furrows giving the impression that the new generation, on leaving the maternal burrow, disperses in all directions.

The first specimens recorded of the last, or fourth, nymphal instar were collected on the 11th November.

The Adult (Pl. I, fig. 2).

The first adult crickets were recorded early in December, and imagines have been recorded between December and early March, but the duration of adult life under natural conditions has not been ascertained.

The ratio of males to females indicates that probably the male sex is more abundant. On the 30th January 1950, 88 crickets (19 females and 69 males) were brought to the laboratory, but on dissection only 35 of the males exhibited spermatophores.

Growth Measurements.

Although no serious attempt has been made to breed the cricket from egg to adult in the insectary, the casual collecting of crickets in the fields from May 1949 onwards has produced some information about the life-cycle and the progress of growth. The results obtained from the measurement of 190 specimens (Table I) indicate that the rate of growth is rapid at the beginning of the life-cycle (April–May) but slows down very considerably during the long and dry winter period (June–October). During the third and fourth (final) nymphal stages the increase

* The female of the well known American Field Cricket, *Acheta* (=*Gryllus*) *assimilis* F., commonly produces about 300 eggs (Metcalf & Flint, 1951).

in body length, and especially weight, is rapid; it is at this time (November–December) that the damage is done to the young plants of tobacco, maize, etc., because the natural food resources (weeds, etc.) have been removed or are reduced to a bare minimum to promote the growth of the plants under cultivation.

TABLE I.

Approximate growth measurements.

Month	Stage	Average length of body (mm.)	Length of crickets (mm.)		Approx. depth of burrows (cm.)
			Min.	Max.	
March	egg	3·1	3·0	4·0	60–80
April	nymph (1st)	5·2	5·0	14·0	2– 5
May	nymph	11·7	9·0	14·0	5–10
June	nymph	13·9	10·0	16·0	10–20
July	nymph	18·0	16·0	21·0	15–30
August	nymph	21·7	16·0	27·0	15–35
September ..	nymph	24·7	23·0	28·0	20–40
October	nymph	27·0	21·0	35·0	30–50
November	nymph (4th)	35·5	22·0	51·0	40–60
December	adult	43·9	34·0	51·0	50–80
January	adult	—	—	—	50–80
February	adult	—	—	—	50–80

The Life-cycle (fig. 1).

B. membranaceus has one generation a year, the adults dying off between February and April, the females having laid their eggs in February and March.

The newly hatched crickets appear to leave the burrow of the parent mother and spread over the surface area in the immediate vicinity, preferring uneven or broken-up surfaces as these facilitate digging. Encrusted surfaces are avoided

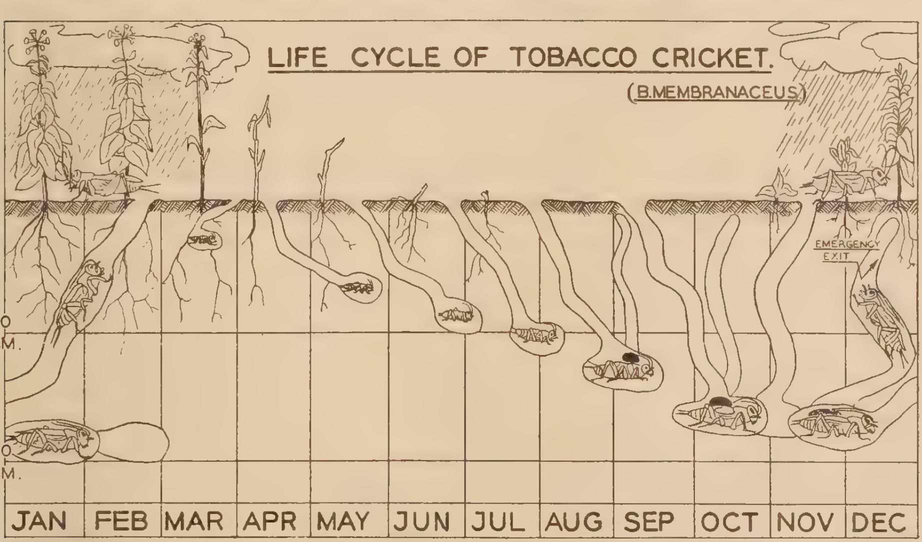

Fig. 1.—Diagrammatic drawing of the life-cycle of *B. membranaceus*.

and the soft and moist conditions of sandy soils generally are most favourable for quick burrowing. The entrance to the burrow is usually concealed in the bush by leaf mould and in the clearings by weeds with prostrate leaves or rosette-forming habits, such as *Helichrysum argyrosphaerum*.

The initial survival potential of young crickets is primarily dependent on the soil-moisture content prevailing after the hatching of the eggs, and also on the activities of natural enemies (Bünzli & Büttiker, 1955) which are facilitated by the very shallow nature of the burrows.

The incidence, pattern of distribution and degree of infestation are probably determined to a considerable extent by the spread and settling of the young larvae and more information is required on this initial phase of the life-cycle.

From observations made during the period 1949–1952 it appears that a sequence of two or more seasons of low rainfall favours *B. membranaceus*, as it has been noted that an excess of moisture in the burrows may cause the crickets to leave them and appear on the surface.

No actual migration over either short or long distances has been noticed. It is thought, however, that both nymphs and adults could leave an over-crowded area, if food supplies became short. In several cases, such migration has been suspected but remains unconfirmed.

Method of Locomotion and Digging.

Due to the exclusively nocturnal activity of the cricket, and its solitary habit, actual observations of the behaviour under natural conditions are scanty. The opportunity was taken, however, of watching the insects in action, in the field as well as in the insectary, by depriving them of their habitual abode and exposing them to daylight. When an adult is exposed, it hurriedly jumps away, and in order to extend the first successive leaps as much as possible, it uses the fluttering action of the wings. Being lucifugous and very intolerant of dry heat, it searches anxiously for a hiding place and, in a ridged tobacco field with no prostrate vegetation, it will follow the slanting banks of a furrow. As soon as a suitable unevenness, such as a protruding clod of earth, is encountered, it stops running and starts digging at once. If all goes well, it will disappear in less than a minute but if, on the other hand, the first attempt is abortive, due to some obstruction, it will move on and make a fresh attempt elsewhere. The operation is performed with the mandibles and forelegs, the latter throwing the loosened earth sideways and backwards. Thrusting ahead horizontally, the earth is pushed backwards underneath the body and to get rid of this excavated earth, the powerful hind legs send the grains and dust flying into the air, the heavier particles settling down on the base and wall of the opposite ridge. Accumulations of earth in the burrow are similarly disposed of periodically when necessary. Observations made in the insectary, where crickets were kept in confinement in specially constructed sand-filled cages (Pl. I, fig. 3), revealed that, as soon as the tunnel has grown in depth, the sand excavated in front and moved backwards is no longer disposed of forcibly by the hind legs. The insect, somehow or other, reverses the position of its body and, in the apt description of D. G. Ashby (Report on soil pests of tobacco, covering period September 1948–March 1949.—Unpublished report, Tob. Pest Control Scheme, Salisbury, S. Rhod., 1949), "' the head is then kept rigidly square on to the body and the whole mass of earth is literally bull-dozed up the surface. If all the earth is not pushed out the first time, further attempts are made. The broad mandibles are most important in this earth moving operation.'' It is obvious that the main moving force again resides in the very muscular hind legs. The final result of the subterranean operations is betrayed on the surface by a steadily-growing, more or less conical dump of loose earth, attaining ultimately a maximum height of 30 cm. on flat ground. These mounds, however, are liable to be disturbed at any time

by animals, wild and domesticated, or by rain, and they may even be levelled or completely washed away. It is of interest to note that within a given area, the periodic expulsion of earth and the opening or closing of the main entrance hole occur simultaneously on almost all the existing burrows within the area, indicating that the population responds promptly to varying environmental conditions. The sorties for collecting fodder also seem to be related to definite meteorological factors. There are no exits during and immediately after heavy or protracted rains, and the store of food in the burrows proves useful at such times.

The activities of the crickets in the substratum are conducive to a partial rejuvenation of the surface soil layer, and in addition, the improved aeration of the subsoil, allowing for enhanced absorption of rain, promotes, under the conditions prevailing in savannah country, the growth of deep-rooted, woody plants.

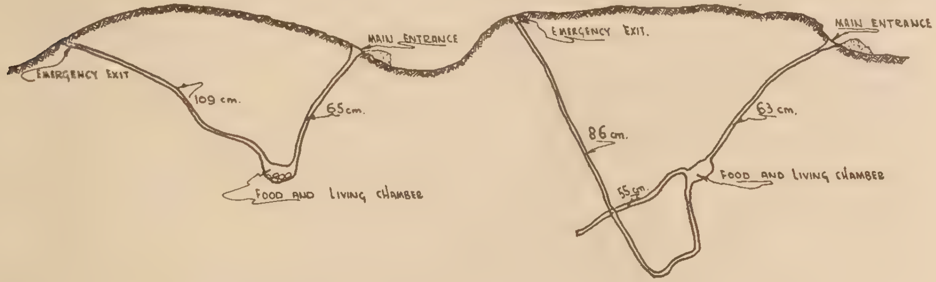

Fig. 2.—Section through two different hole systems of *B. membranaceus*. Figures indicate lengths of the various sections of the tunnels.

The Burrow System (fig. 2).

The burrows excavated by the juvenile crickets have one main hole for entrance and exit. In the case of flat, levelled soil it leads gradually down to the main dwelling chamber, in slightly undulating soil (old ridges) or an otherwise uneven soil surface, the upper part of the channel is usually aligned in such a way as to give the shortest access to the surface, thus facilitating the disposal of the excavated earth.

The tunnels dug by the very young crickets are very narrow in diameter, conforming to the tiny bodies, but run almost horizontally, or more often slanting slightly downwards. There seems to be no emergency-exit hole but sometimes more than one orifice is present. The store chambers are primitive, being merely rough enlargements of the runs.

In September and October, when activity increases, an emergency exit, superficially not detectable, is excavated in addition to the existing old main entrance hole. The latter is very often found, at least temporarily, completely blocked with loose soil; this factor probably operates against predacious invaders which become active at this time of the year. Keeping the orifice of the main entrance alternatively closed or open might also be linked up with moisture-temperature conditioning of the burrows. The emergency exit is mostly covered with sand.

The greatest concentration of cricket burrows is to be found in uncultivated virgin land or in border strips inside and outside relatively small cultivated areas; in some instances we were able to record up to four and five cricket holes per square yard. Inside large areas of cultivated land the number of crickets is, as a rule, very much smaller, but ridges with their ditches or contour ridges harbour more crickets, particularly in the upper parts of such fields. The irregularity in the distribution over a field is also influenced by the texture and structure of the surface.

The Food, Food-collecting and Storage.

B. membranaceus subsists on an entirely vegetarian diet,* taking the area immediately surrounding the fixed burrow for its foraging ground. The food found stored in the subterranean chambers gives a fairly true picture of the vegetation readily available (Table II).

TABLE II.

Plant material stored by *B. membranaceus*.

Hole no. 1	12 msasa * leaves
2	3 msasa leaves
3	3 msasa leaves and 3 woody sticks (small)
4	6 msasa leaves, woody sticks and msasa sprouts
5	12 msasa leaves, 10 parts of tobacco leaves
6	Many msasa leaves and sprouts
7	Many sunnhemp leaves and stalks
8	Many msasa and mnondo† leaves and twigs, tobacco, young cut plants (stems and leaves)
9	14 msasa leaves, 1 msasa pod, 18 beans (seeds) and 1 woody stalk
10	Several sunnhemp leaves and stem
11	Several sunnhemp leaves and flowers
12	20 msasa leaves (fresh)
13–18	Tobacco leaves
19	Grass, miscellaneous weed species
20	1 msasa leaf and 12 shrivelled leaves (indet.)

* *Brachystegia spiciformis*. † *Isoberlinia globiflora*.

These results, which show a much wider range than those recorded by Chorley (1946) and Ashby (*loc. cit.*), require some comment. Drastic differences between the wet and dry seasons are responsible for a succession of succulent and dry vegetable matter upon which the cricket, which is active all the year round, has to subsist. Under virgin bush-veld conditions and in a favourable season, mainly lush grasses and herbs, seedlings and root suckers of the trees, *Brachystegia spiciformis* (msasa) and *Isoberlinia globiflora* (mnondo), are cut off at ground level and dragged to the burrow. In the dry season, however, dried plant material is collected, especially the leaves of the same indigenous trees which are scattered all over the ground and partly wind-blown into open spaces. In cultivated land, with semi-annual crops such as tobacco, maize, field beans, green manure and garden vegetables, the seedlings and young transplants are cut and stored. As soon as the stems of such plants have hardened up and acquired immunity against further attack—*B. membranaceus* never climbs plants to get at tender parts as do young larvae of the common Noctuid (cutworm) *Agrotis segetum* (Schiff.)—the regrowth of imperfectly uprooted bushes and trees, adventitious weeds such as *Helichrysum argyrosphaerum* (Compositae), *Gisekia pharnaceoides* (Molluginaceae) and various grasses are cut. During the dry season (May to October), the residues of the above-mentioned plants (if not ploughed in) are collected by the insects, and eventually fallen leaves of trees that are usually kept as fireguards or wind belts and often surround individual fields on all sides. The most profuse breeding of the young cricket population, however, was observed in an abandoned tobacco field where the pulled stalks, bearing ample sucker growth, were left lying in the furrow. Counts taken of cricket holes in this field in August 1951 and in the adjacent fallow land gave 6,120 and 2,684 burrows per acre, respectively.

* Cannibalistic habits develop only when crickets are kept in captivity.

To sum up, the period of dry and often scarce food material, from June to October, is associated with slow nymphal development. From November to May, however, there is plenty of young and succulent plant growth which the insects cut for food and this period coincides with the more rapid development of the pre-imaginal and adult stages of development.

The food collected at different times of the year is by no means always fit for immediate consumption and it has to be made more palatable. It may carry either too much or too little moisture. The conditioning of raw material that is too succulent may be begun outside the burrow and the natural wilting resulting from the so-called "wasteful cutting" of several plants in tobacco and maize fields as well as in vegetable gardens, whereby the majority of the severed seedlings is left *in situ* on the ground, is thought to be for this purpose. The prevailing conditions of restricted space and limited possibilities for ventilation appear to prohibit the withering in bulk of freshly cut food in the store chamber on account of the risk of the development of mould and of fouling the air, although a small subsidiary cavity is sometimes available. On uncultivated land, when the weather is dull and soil conditions are rather humid, it has been observed that quite rigid blades of grasses and fully turgescent bigger leaves are pulled partially into the funnel of the entrance hole, sticking out of the orifice like a bouquet.

In fields where the tobacco is at an early stage of growth, cutworms (NOCTUIDAE) and false wireworms (TENEBRIONIDAE) may be present as well as the crickets, and inspections carried out at short intervals revealed that plants severed by the former insects are readily picked up by the crickets. The general preference for vegetable matter lying loose on the soil surface also explains the very good results obtained with poisoned baits consisting of suitably treated, chopped-up, green plants scattered amongst the stands of young tobacco still prone to be attacked by the cricket. In such instances, the wilted green bait was carried away and the living plants left alone.

During the cloudless winter season when dead, dry plant residues only are available, the dew at night-time softens the brittle food.

The final conditioning which renders the plant material, whether it is collected wet or dry, palatable and fit for storage always takes place in the burrow. Observations revealed that foraging is strictly confined to the night-time and that meals are always taken in the shelter of the dwelling. The food to be stored is not chopped up into small pieces but left in its original form, and is compacted into the hindmost part of the cavity. Comparatively large tobacco leaves are drawn into the entrance hole where they become rolled into the form of a tube. It is therefore not surprising that occasionally one finds the walls of the store chamber entirely coated with such material.

Sometimes large seeds such as maize grains, seed capsules of tobacco, rolled up pieces of pods of cultivated and indigenous leguminous plants, and pieces of stalks and twigs are also brought into the burrow and compacted with the usual leafy food.

Although the food stored was crumpled and soft to the touch, it could be easily unfolded and was never found in a mouldy or fermenting condition.

Actual feeding was not witnessed, but dissections of the gut indicated that the food is triturated to a compact pulpy paste, the excreta consisting of pellets which are longer than broad.

Summary.

The Tobacco Cricket, *Brachytrupes membranaceus* (Dru.), is a pest of young plants of tobacco, maize and other field and garden crops in Southern Rhodesia. During the period of investigations, 1949–52, it was found to be widely distributed in the Territory, the heaviest attacks occurring in areas of light sandy soil of granitic origin. All stages are nocturnal and each individual excavates and

inhabits a permanent burrow in the soil, that of an adult averaging 50 to 80 cm. in depth. The burrow has an enlarged chamber in which the cricket lives and stores food.

There is one generation a year. Oviposition takes place in February and March, the average number of eggs per female, as shown by dissection, was 216. Incubation takes about 30 days and development of the young nymphs is at first rapid. From June to October, the period of dry and often scarce food, development is retarded but increases rapidly during the third and fourth (the last) nymphal stages in November. From November to May, when young and succulent food abounds, development is rapid. The adults start appearing early in December.

The eggs are laid in the burrows and the young nymphs on hatching crawl away from the parent burrow, in all directions, in search of suitable places in which to start digging. The mandibles are used to excavate the soil which is thrown outwards by the forelegs, and the mounds formed by the time the adult stage is reached may attain a height of as much as 30 cm. When an adult is evicted from its burrow, as soon as it finds a suitable place to dig, it will disappear within the space of a minute.

The burrows may be found in virgin land or in cultivated land, or along the borders of cultivated fields. The food consists of succulent or dry vegetable matter, according to the time of year, and is carried to and stored in chambers in the burrows. In the virgin veld it consists mainly of lush grasses, seedlings and root suckers of trees such as *Brachystegia* and *Isoberlinia* in the rainy season and of dried material of a similar nature during the dry months. In cultivated land, tobacco, maize, field beans, garden vegetables, seedlings and young transplants are cut and stored.

Although the food is compacted in chambers in the burrows it has not been found in a mouldy or fermenting condition. It is thought that it is conditioned before storage, the more succulent material being allowed to wilt before being taken into the burrow and the dry material when softened by dew.

Acknowledgements.

We extend our thanks to the Rhodesia Tobacco Association and the Directors of Fisons Pest Control (C.A.), Ltd., for permission to publish this paper.

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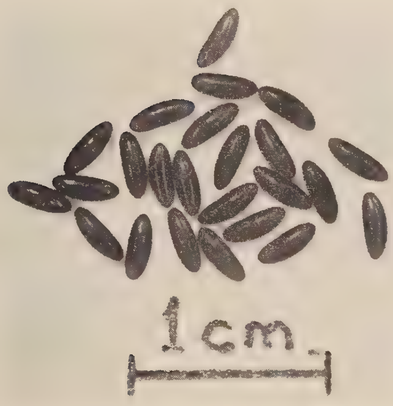

FIG. 1. Eggs of *Brachytrupes membranaceus* (enlarged).

FIG. 2. Adult female of *B. membranaceus* (slightly enlarged).

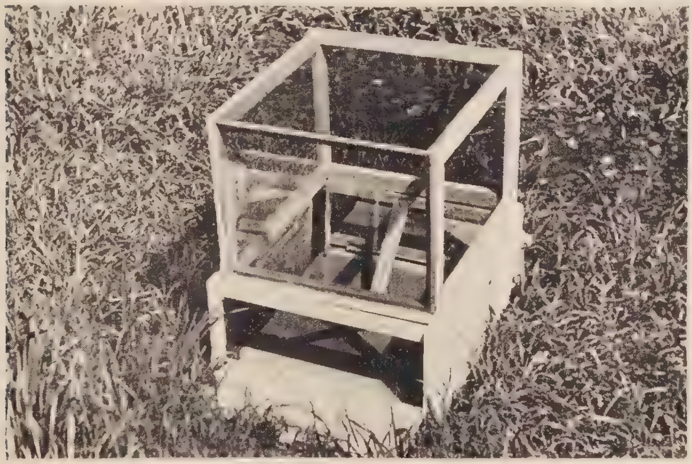

FIG. 3. Cage used for laboratory observations on behaviour and oviposition of *B. membranaceus*.

CONTRIBUTION TO THE STUDY OF SOME PHYTOPHAGOUS ACARINA AND THEIR PREDATORS IN MAURITIUS.

By. L. André Moutia
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This work was started early in 1952, when heavy attacks of red spiders were reported on tomato, egg-plant, potato, bean and other crops which hitherto were almost free from these pests. The factors responsible for this sudden increase in the mite population have been discussed in a previous paper (Moutia, 1953).

In order to throw more light upon this complex problem a thorough survey of the phytophagous mite fauna was carried out. This preliminary work was followed by the study of the bionomics of some economic species and their predators.

Collecting of specimens for identification extended over a period of four years. The list drawn up therefrom cannot pretend to be in any way complete but it can at least be considered to present a fair picture of the phytophagous mite fauna and of its predators in Mauritius.

I. Annotated List of Species.

Previous to this work, only five species of phytophagous mites had been recorded from Mauritius, *viz.:—Hemitarsonemus latus* (Banks), *Raoiella indica* Hirst (Moutia, 1955), *Steneotarsonemus bancrofti* (Michael) (cited as *Tarsonemus spinipes* Hirst *), *Eriophyes* sp. (cited as *Phytopus* sp.) and *Tetranychus telarius* (L.) (Moutia & Mamet, 1947). Of these species, *Tetranychus telarius* has not been collected during the present extensive survey. The record of it should be considered as a misidentification for one of the other species of *Tetranychus* mentioned below.

Thirty species are here recorded from Mauritius, of which 21 are phytophagous and nine mainly predacious in habit. The two families most numerously represented are the Tetranychidae (ten species) and the Eriophyidae (five species).

Many of these species are either new or are still awaiting a final identification. Owing to their agricultural economic importance, it has been considered advisable to record them in this study.

A. Tetranychidae.

Petrobia harti (Ewing).

A species collected mostly on *Oxalis* sp., causing fine stippling on leaves which turn almost yellow. Sometimes found on leaves of sugar-cane in contact with infested *Oxalis*. Colonies on sugar-cane do not appear to thrive or multiply, and cause no serious damage to this plant.

Petrobia sp.

A species of *Petrobia* believed to be new was recorded on *Verbena bonariensis*, a weed growing along road borders and in cane-field pathways; its attacks, when severe, cause a slight stunting of its food-plant.

No predators were found on these two species of *Petrobia*. Heavy rains cause an appreciable reduction of their populations.

* Synonymy according to Mr. D. Macfarlane.

Eutetranychus banksi (McG.).

This species is common on the upper surface of leaves of *Citrus* spp., especially lemon (*C. aurantiifolia*), also on peach, loquat (*Eriobotrya japonica*), and on "karapoucha" or curry-leaf tree (*Murraya koenigii*). Severe infestation on *Citrus* leaves, which is characterised by numerous very fine stipplings, usually causes them to fall prematurely. Under similar conditions, leaves of other food-plants sometimes show a bronze-like appearance. No predatory mites recorded. Heavy rain is a limiting factor in the distribution of this species.

Eotetranychus sp.

This mite, which is believed to be new to science, is found on the under surface of apple leaves, along the veins; it forms small colonies which, when abundant, cause a crinkling of the leaf. The following predators were found feeding on this mite: a *Scolothrips* sp. in fairly large numbers, and a *Typhlodromus* sp.

Colonies of this mite are very rapidly destroyed by these two predators. As a consequence, attack on apple is, on the whole, rather insignificant.

Oligonychus biharensis (Hirst).

This species was collected on the upper surface of leaves of mango, litchi, *Cotoneaster*, loquat, longane (*Euphorbia longana*) and camphor (*Cinnamomum camphora*). Its attacks are sporadic and cause no great damage to these plants, except that leaves severely attacked show numerous white specks at places where feeding has occurred. On loquat, a dark bronzing of the leaf is characteristic of the attack. The Coccinellid, *Stethorus vinsoni* Kapur, and a species of Cecidomyiid are two efficient predators of this species.

Oligonychus mangiferus (Rahm. & Sapra).

Specimens of a species of mite which occurred mainly on the upper surface of leaves of mango, loquat and peach were sent to Dr. E. W. Baker, of the United States Department of Agriculture, who compared them with Indian material of *O. mangiferus* and considered them to be the same. The Mauritian species sometimes occurs in association with *O. biharensis*. When severely attacked, mango leaves dry and fall prematurely. The same predators as are found on *O. biharensis* feed occasionally on this species.

Oligonychus sp. (*pratensis* (Banks) group).

Small colonies of this species are usually to be found on the lower surface of coconut leaves along the midrib. When feeding has been severe, long yellowish patches may be observed at the points of attack. Infestation is sporadic and sometimes occurs conjointly with attacks of *Raoiella indica*.

This mite was also collected during the dry months on sugar-cane growing in greenhouses. In the fields it was found on "fataque" (*Panicum maximum*) and on maize. A species of *Typhlodromus* that is new to science preys upon this species. Larvae of a species of Cecidomyiid are occasional predators of colonies found on sugar-cane in greenhouses.

Tetranychus cucurbitae Rahm. & Sapra.

This species was recorded mainly on peach plants, causing a pronounced yellowing of the leaves, which fall prematurely. On coconut its attacks are sporadic and cause no great damage, being generally brought under control by two predatory mites, *Typhlodromus* sp. and *Typhlodromus caudatus* (Berl.).

It is interesting to note that *Tetranychus cucurbitae* does not have a very wide range of food-plants in Mauritius as compared with India, where 60 different plants are hosts of this species (Rahman & Sapra, 1946).

Tetranychus sp. (*ludeni* Zacher group).

This red spider, which is believed to be new to science, is a serious pest of bean, pumpkin (*Cucurbita maxima*, *Cucurbita pepo*) and other cucurbitaceous plants, as well as of *Hibiscus esculentus*. It is often found in association with another species, *Tetranychus marianae* McG., on egg-plant (*Solanum melongena*). It is very destructive to these plants; attacked leaves show a pronounced yellowish hue, wilt and drop fairly rapidly, particularly when drought prevails. The following predators are fairly abundant when infestation is at its peak:—*Scolothrips* sp. near *indicus* Priesn., *Stethorus vinsoni*, *Oligota pallidicornis* Cam. and *Feltiella* sp. near *tetranychi* Rübs.

Tetranychus marianae McG.*

This species is very destructive to tomato (*Lycopersicum esculentum*), egg-plant (*Solanum melongena*), potato (*Solanum tuberosum*), peanut (*Arachis hypogaea*) and *Solanum nigrum*. Other plants which generally resist the attack of this mite and act as potential reservoirs are *Solanum auriculatum*, *S. indicum*, *Ipomoea batatas*, *Asystasia coromandeliana* and *Capsicum annuum*. Predators of this species are the same as those mentioned under *Tetranychus* sp. (*ludeni* group). The bionomics of this species and of its predators are discussed later.

B. **Tenuipalpidae** (= Phytoptipalpidae).

Brevipalpus phoenicis (Geijskes).

This species has a very wide range of food-plants. It is found on *Citrus* sp., tea (*Thea sinensis*), chilli (*Capsicum annuum*), *Cotoneaster* sp., coffee (*Coffea arabica*), peach, papaya (*Carica papaya*), loquat, coconut, geranium (*Pelargonium zonale*), *Hibiscus esculentus*, *Solanum indicum*, *Bidens pilosa*, apple, pear, *Livistona chinensis*, *Verbena bonariensis*, privet (*Ligustrum walkeri*) and olive (*Olea europea*).

Large numbers of this mite are sometimes found on *Citrus* and tea plants; no very conspicuous damage has been noticed on these plants, but the species sometimes causes a slight scarring on *Citrus* fruits and blisters on leaves of tea.

Attention should be given to this mite in view of the fact that a related species, *Brevipalpus inornatus* (Banks), is believed to bring about, in countries where it occurs, a serious disease of *Citrus*, known as " lepra explosiva ", which is caused by a toxin secreted by this species during the process of feeding (Vergani, 1945).

No predator was found on this mite. Breeding of *B. phoenicis* on leaf-disc culture (as described in another section of this work) gave the following results (in days) for a summer generation (mean temperature 23·4°C.):—egg stage, 5; larva, 4; protonymph, 7; deutonymph, 6, *i.e.*, a cycle of 22 days from egg to adult. The pre-oviposition period was 4–5 days. In winter (mean temperature 17·5°C.) the cycle from egg to adult was 35 days:—egg, 11 days; larva, protonymph and deutonymph 7, 8 and 9 days, respectively; the pre-oviposition period was from 9–10 days. The eggs are laid in clusters in old moulted skins or in crevices or abrasions on the under surface of leaves. The number of eggs per cluster varies from 4 to 6, the maximum number of eggs per cluster being 15. No figures for the total number of eggs laid per female could be obtained as most of the adult mites laid their eggs sparingly on portions of the leaf disc.

Raoiella indica Hirst.

This species, which appears to be of relatively recent introduction, is now prevalent in most of the coconut plantations in the island. It has also been found on the palm (*Dictyosperma alba*), and on date palm (*Phoenix dactylifera*). Young

* Mauritian specimens according to Dr. E. W. Baker show differences from *marianae* but he is not satisfied that they warrant specific status.

coconut plants are more severely affected; plants over five years old seem to resist the attack of this mite. Sometimes older plants grown in conditions of poor drainage and in soil deficient in mineral and organic matter are particularly affected.

Its main predator is *Typhlodromus caudatus.*

Phyllotetranychus sp.

Probably a new species. Found on the under surface of leaves of *Latania loddigesii.* No other food-plant recorded and no predators found. Climatic factors, mainly summer rains, partially check this mite.

C. Tuckerellidae.

Tuckerella pavoniformis (Ewing).

A phytophagous species recorded on *Cotoneaster* and papaya; not found in abundance on these plants and is not of economic importance. It is sometimes found in association with *Oligonychus biharensis* on *Cotoneaster.*

D. Eriophyidae.

Phyllocoptruta oleivora (Ashm.).

This mite is sometimes found in thousands feeding on leaves and fruits of *Citrus*, causing in the latter a pale brownish to black discoloration or russeting. Not of great economic importance at the present time, but should be considered as a potential menace to large-scale cultivation of *Citrus* in Mauritius. No predator recorded. The population of this mite suffers a marked reduction during the winter season.

Calacarus carinatus (Green) (= *Calacarus adornatus* (Keifer)).

This vagrant mite feeds on chilli (*Capsicum annuum*), on which it causes a slight bronzing of the leaves. Abundant in the dry and hot regions.

A species of the Tribe Diptilomiopini.

This species is sometimes found in very large numbers on the under surface of sugar-cane leaves but apparently causes no harm. Heavy showers bring a great reduction in the population of this mite. A species of the Bdellidae was found preying on this Eriophyid.

Tegonotus sp.

Very common on tomato leaves and stems. Severe infestation is generally associated with a bronzing of the leaves. Hot and dry weather conditions favour the development and spread of this mite.

Abacarus sp.

This species was found on sugar-cane in association with another species of the Tribe Diptilomiopini. No observations were made on this mite.

E. Tarsonemidae.

Hemitarsonemus latus (Banks).

This mite has a very wide range of food-plants comprising the following:— bean, vohems (*Vigna unguiculata*), potato, tomato, egg-plant, chilli, *Solanum indicum*, water-cress, Swiss chard (*Beta vulgaris cicla*), *Citrus*, avocado, peach, mango, papaya, tea (*Thea sinensis*), *Begonia*, *Brunfelsia hopeana*, *Dahlia*, *Geranium*, etc.

Its presence is revealed by the sudden curling and crinkling of leaves, rather suggestive of a virus condition, followed by blister patches. Plants severely attacked stop growing and die.

On tea, the mite is generally washed off the leaves by heavy rain during the summer months. On chilli, the predator, *Typhlodromus ovalis* Evans, checks this mite very effectively. No other predator was found on the other plants. The life-cycle is of very short duration, being 4–5 days during summer and 7–10 days in the winter months (temp. 28–30° and 18–20°C., respectively).

Steneotarsonemus bancrofti (Michael).

This mite is relatively rare in sugar-cane fields and is of very minor importance. It is found between the leaf sheath and the cane stalk, either on the tender upper parts of the plant or embedded in the epidermis and buds where it forms blister-like enations on the surface.

No predators have been recorded. Climatic factors appear to bring about a natural check.

F. Phytoseiidae.

Typhlodromus (*Amblyseius*) *ovalis* Evans.

A common predator of *Hemitarsonemus latus*, especially on chilli; it feeds mainly on eggs of this mite and very occasionally on the young stages. It also attacks various Eriophyids on sugar-cane and on *Panicum maximum*. This predatory mite was not found attacking *H. latus* on various other food-plants of economic importance. *viz.*:—tea and water-cress. A species which reproduces itself quickly; egg to adult in summer: 4–6 days.

Typhlodromus (*Amblyseius*) *caudatus* (Berl.).

A very active predator of the coconut mite, *Raoiella indica*; also found attacking *Tetranychus cucurbitae* on peach, *Tetranychus marianae* on egg-plant and *Solanum nigrum*; and *Eotetranychus* sp. on apple. It feeds mainly on eggs and young stages and rarely on adult mites.

Typhlodromus sp.

A species sometimes found attacking *Oligonychus* sp. (*pratensis* group) on sugar-cane and coconut.

G. Miscellaneous Species.

Asca sp. (Digamasellidae).

A predator of *Tetranychus marianae* on *Solanum nigrum* and *Solanum indicum*. Not very common.

Kleemannia sp. (Aceosejidae).

Collected on egg-plant infested with *Tetranychus marianae*. No observation made on its rôle and activity; most probably a predator.

Gen. et sp. indet. (Bdellidae).

Material of a single species of Bdellid (gen. et sp. indet.) was found in association with Eriophyids on sugar-cane and *Panicum maximum*.

Histiostoma sp. (Anoetidae).

A predator of Eriophyids on sugar-cane.

Phauloppia sp. (Oribatulidae).

Common on leaves of peach, *Cotoneaster*, mango, sugar-cane and various other plants. It does not seem to be a phytophagous species, but probably lives as a scavenger on leaves previously attacked by other species of mites.

Galumna sp. (GALUMNIDAE).

Found at the base of coconut trees and in cracks and crevices of "filao" (*Casuarina*) bark. Its rôle has not been determined.

TABLE I.

Geographical distribution of the mites specifically identified from Mauritius.

Species	Geographical distribution
Petrobia harti	U.S.S.R. (Georgia), Japan, Egypt, Southern Rhodesia, Australia (New South Wales), U.S.A. (Alabama, California, Connecticut, Florida, Illinois, Maryland, Mississippi).
Eutetranychus banksi	Italy, Cyprus, Israel, India, Egypt, Libya, Kenya, Portuguese East Africa, Union of South Africa, Sudan, U.S.A. (Florida, Texas), Mexico, Argentina, Peru.
Oligonychus biharensis	India, Hawaiian Is.
Oligonychus mangiferus	India, Hawaiian Is.
Tetranychus marianae	Fiji Is., Mariana Is., U.S.A. (Florida, Texas), Nicaragua, Argentina.
Tetranychus cucurbitae	Ceylon, India, Kenya, Tanganyika, Fiji Is., Hawaiian Is., U.S.A. (New York, Florida), West Indies (Bahama Is., Porto Rico), Venezuela.
Brevipalpus phoenicis	Ceylon, Cyprus, India, Malaya, Kenya, Tanganyika, Australia (Queensland), New Zealand, Hawaiian Is., U.S.A. (California, Florida, Washington), West Indies (Cuba, Trinidad), Argentina.
Raoiella indica	Egypt, India.
Tuckerella pavoniformis	Australia (New South Wales), Hawaiian Is., U.S.A. (California).
Phyllocoptruta oleivora	China, Cyprus, Formosa, Israel, Japan, Lebanon, Persia, Philippine Is., Syria, Turkey, U.S.S.R. (Transcaucasia), Kenya, Mauritius, Tanganyika, Australia (New South Wales, Queensland, Western Australia), Cook Is., Fiji Is., Hawaiian Is., Mexico, U.S.A. (Alabama, California, Florida, Louisiana, Mississippi, Texas), Guatemala, West Indies (Bermuda, Cuba, Jamaica, Porto Rico), Argentina (Buenos Aires, Chaco, Corrientes, Entre Rios, Formosa, Misiones, Santa Fé, Tucumán), Brazil (Bahia, São Paulo), Ecuador, Peru, Venezuela.*
Calacarus carinatus	Ceylon, U.S.A. (California, "southern states").
Hemitarsonemus latus	Britain, Germany, Holland, Norway, Switzerland, Ceylon, Formosa, India, Indonesia (Sumatra, Java), Malaya, Philippines, Belgian Congo, French Equatorial Africa, Tanganyika, Uganda, Union of South Africa, Australia (New South Wales, Queensland), Hawaiian Is., Mariana Is., Canada (Ontario), U.S.A. (California, Connecticut, Florida, Illinois, Massachusetts, New Hampshire, New Jersey, New York, Washington), West Indies (Bermuda, Cuba, Porto Rico, Trinidad, Virgin Is.), Brazil.
Steneotarsonemus bancrofti	Philippines, Australia (Queensland), Hawaiian Is., Society Is., U.S.A. (Florida, Louisiana, Virginia), West Indies (Barbados Is., Porto Rico).
Typhlodromus caudatus	Java, Kenya, British Guiana.
Typhlodromus ovalis	Malaya.

* Mainly taken from Commonw. Inst. Ent. Map no. 78 (1957).

II. Geographical Distribution.

It is rather difficult to discuss this topic here in as much as many of the mites mentioned in the text have not been identified to specific rank. A rough idea of the distribution of the fully identified species can nevertheless be obtained on consulting Table I. Most of the information has been taken from the work of Pritchard & Baker (1955), and complementary notes were kindly supplied by Mr. D. Macfarlane of the Commonwealth Institute of Entomology.

It appears that South and East Africa, India, the Hawaiian Islands, Australia and Egypt are most probably the main sources from which the phytophagous mite fauna of Mauritius originated. The date and possible ways through which these various species were introduced is largely a matter of conjecture.

III. Bionomics of some Economic Species.

Method of Breeding.

The detached-leaf culture method as used by Rodriguez (1953) was employed throughout this study. It consists in the following: cleaned and well washed leaf discs, 18–25 mm. in diameter, are placed in individual petri dishes containing sufficient 2 per cent. sucrose solution to allow the disc to float freely. The female mite is introduced thereon with a fine camel-hair brush. The leaf disc will remain in perfect condition for from 4 to 15 days according to the various types of leaves used. Bean-leaf discs last from 6 to 8 days in the sucrose solution and were found more suitable than leaves of egg-plant, tomato, chilli and *Hibiscus* for the study of the development of the various stages of *Tetranychus marianae*. Discs of coconut leaves remained in good condition for three weeks; this advantage was made full use of for breeding *Raoiella indica* and its predator, *Typhlodromus caudatus*. All petri dishes were kept in small glass cages 30 × 30 × 55 cm., with top and door covered with fine-mesh wire gauze. This precaution was taken against cockroaches, flies, etc., which otherwise would have alighted on the discs and spoiled the cultures. These cages were exposed to daylight, but not to direct sunlight.

Life-history of *Tetranychus marianae*.

This mite, which is a pest of tomato, egg-plant, etc. (see p. 61), feeds, as do other web-forming Tetranychids, by inserting its mouth-parts into a leaf cell and sucking out its contents including the chlorophyll. Small white spots develop around each feeding puncture and these subsequently form larger patches on the leaves, which turn yellow, dry up and drop, thus bringing about premature death of the plant. The web is spun on the lower surface of the leaves and may cover the whole plant completely when infestations assume large-scale proportions. Plants in dry regions are more particularly affected by the attacks of this mite.

Many secondary food-plants (list given on p. 61) survive the attack of this mite and are its main food reservoirs when tomato plants are scarce in the field. Eggs are generally laid on the under surface of leaves of the food-plants in the field; but, when infestations become dense, they are also laid on the upper surface of leaves and on stems. Nearly 100 per cent. of the eggs hatch; the young larvae start feeding almost as soon as they hatch. Each moult is preceded by a quiescent stage of 12–24 hours. Both male and female individuals pass through two nymphal stages. Males emerge 24–36 hours before females and await the females as they emerge from the deutonymphs, when copulation takes place. The duration of the copulating act varies from 3 to 25 minutes. A female mite may mate more than once during her lifetime. The pre-oviposition period in summer (temp. 24·7–28°C.) is of 2–5 days, and in winter from 6 to 8 days (temp. 14–17°C.). The number of eggs laid per female in leaf-disc cultures

varied from 105 to 146 (the mean being 124·5) during a period of 32–35 days. The maximum number of eggs laid in one day per female was 15, the mean number being 4·1. The average length of life of the adult female was 41·5 days (maximum 43); the males generally died a few days before the females. The post-oviposition period varies from 6 to 10 days. Deutonymphs sometimes start the early spinning of the web. The mean duration of the various stages is summarised in Table II.

TABLE II.

Duration of various stages in the life-cycle of *Tetranychus marianae* in summer (Oct.–Mar.) and in winter (Apr.–Sept.).

Stage	Summer (mean temp. 22·8 °C.)		Winter (mean temp. 19·4 °C.)	
	Mean minimum (days)	Mean maximum (days)	Mean minimum (days)	Mean maximum (days)
Egg	1	3	6	8
Larva	1	2	3	5
Protonymph ..	1	2	3	4
Deutonymph ..	1	2	3	5
Egg to adult ..	4	9	15	22
Mean period of development	6·5 days		18·5 days	

The shortest life-cycle was observed to occur in January–February (mean maximum temp. 28°C.) and the longest in July–August (mean maximum temp. 21·4°C., mean minimum 15°C.).

Parthenogenetic reproduction, giving only male individuals, was observed to occur in the laboratory, the period of development of these males being the same as that for those obtained from eggs laid by fertilised females.

TABLE III.

Sex ratio in field samples of *Tetranychus marianae*.

Month	No. of individuals		Total	Ratio		
	Males	Females		Males	:	Females
Jan. ..	131	472	603	1	:	3·6
Feb. ..	120	420	540	1	:	3·5
Mar. ..	262	468	730	1	:	1·8
Apr. ..	123	139	262	1	:	1·1
May ..	172	429	601	1	:	2·5
June ..	110	150	260	1	:	1·4
July ..	85	230	315	1	:	2·7
Aug. ..	107	201	308	1	:	1·9
Sept. ..	81	244	325	1	:	3·0
Oct. ..	97	313	410	1	:	3·2
Nov. ..	228	1698	1926	1	:	7·4
Dec. ..	90	513	603	1	:	5·7
Total ..	1606	5277	6883			
			Average	1	:	3·3

The sex ratio was determined from field samples of ten leaves of tomato or egg-plant taken monthly over a year. The results are summarised in Table III.

It is clear, as shown in Table III, that adult male mites are present at all times in sufficient numbers to ensure the fertilisation of all females, as one male is able to fertilise several females. Parthenogenetic reproduction in the field is thus reduced. On the other hand, the high proportion of females found all the year round contributes to the steady increase of this species in the field.

The number of generations, as worked out from field observations and laboratory breeding, is about 24–30 per annum. They are distributed as follows:

TABLE IV.

Number of generations of *Tetranychus marianae* per month.

Months	No. of generations per month	Months	No. of generations per month
January	2–3	July ..	1·5
February	3–4	August ..	1·5
March ..	3–4	September	1·5
April ..	3	October ..	1·5
May ..	1·5–2	November	2–3
June ..	1·5–2	December	2–3
		Total ..	24–30

Rainfall, cyclonic disturbances and temperature are the main climatic factors regulating the population density of this species in Mauritius.

Activity is greatest during the summer months from November to April with an average of 17·5 generations which overlap each other; development is most rapid in February–March. A marked increase in the infestation is noticed in November, which remains high until it is followed by an abrupt fall with the onset of winter in June, after which it remains low for the cool dry winter season from June to October. The temporary fall in population in April, shown in Table III, was due to an unusually cold spell during that month.

Observations have shown that a few days of heavy and continuous rain or a violent gale followed by heavy rains reduce infestation considerably. Young mites —larvae and nymphs—just after moulting and young adult females are particularly sensitive to these conditions. Leaves collected from the field after such disturbances show a high percentage of dead mites, amounting sometimes to over 90 per cent. On the coastal belt, in winter, when the temperature is fairly high and precipitation low, infestation is sometimes very severe on tomato and egg-plant. No diapause or hibernation of any stage of the mite was observed.

Life-history of ***Raoiella indica.***

This red mite is found in very large numbers on the under surface of coconut leaves. The eggs are scattered thereon in colonies ranging from 108 to 330; they are red in colour, oblong, smooth and shiny and measure 0·117 mm. in length and 0·088 mm. in breadth, with a stipe 0·148 mm. long. On hatching, the young larvae are reddish in colour, slow in their movements and at once start feeding on the leaf tissues. Before each moult there is a quiescent period of 24–36 hours. Males and females pass through two nymphal stages. Copulation of female individuals still in the deutonymph stage was, in some cases, observed 24–48 hours before the quiescent period which precedes the last moult. One female may mate with several males during her lifetime; in each case the duration of the act lasts from one to twelve hours. The pre-oviposition period is three days in summer

and seven days in winter. The number of eggs laid per day by one female varies from 1 to 6, with an average of 2. The average number of eggs laid on a leaf disc in the laboratory was 28·1, with a maximum of 38 (on 15 observations) during a laying period of 27 days, which is the average adult life of a female mite; the adult life of the male is 3–5 days shorter.

The duration of the life-cycle, worked out from laboratory rearings on leaf discs, is given in Table V.

TABLE V.

Duration, in days, of various stages in the life-cycle of *Raoiella indica*.

Stage	Feb.–Mar. (mean temp. 24·2°C.)	Mean	July–Aug. (mean temp. 17·9°C.)	Mean
Egg	4–6	5·0	5–8	6·5
Larva	6–8	7·0	9–10	9·5
Protonymph ..	4–7	5·5	6–7	6·5
Deutonymph ..	4–5	4·5	10–11	10·5
Total	18–26	22	30–36	33

The sex ratio varies considerably: in April–May, the proportion was as follows:—101 males: 1,147 females (1 : 11·4) and in October–November, 402 males: 941 females (1 : 2·3).

Mites are generally abundant in the field during the months of September to March, except when heavy showers of rain occur during the months of November to January, when a marked decrease in infestation may be noticed. During the months of April to August there is a reduction in the mite population. Coconut plants during these months nevertheless present a sickly yellowish appearance which may be due mainly to the dry-season conditions prevailing at that time, or perhaps to a complex of biotic factors including some unknown disease which may be of a virus type.

IV. Predatory Enemies.

The most important predators of *Tetranychus marianae* and *Tetranychus* sp. (*ludeni* group) in the Island are the Coccinellid, *Stethorus vinsoni*, and the Cecidomyiid, *Feltiella* sp. near *tetranychi*. Other predatory insects of minor importance are *Oligota pallidicornis*, *Exochomus laeviusculus* Weise and *Scolothrips* sp. near *indicus*.

Scolothrips sp. near *indicus* is mainly a predator of mites on egg-plant, bean and *Asystasia coromandeliana*.

Exochomus laeviusculus is another species that occasionally feeds on mites; its normal diet is Aphids, and it is very seldom found on tomato plants infested with *T. marianae*.

Oligota pallidicornis is a sporadic and erratic predator, found mostly on egg-plant and bean, in very varying numbers; it has only been recorded in very few instances on tomato plants.

The predatory mite, *Typhlodromus caudatus*, is occasionally found feeding on *Tetranychus marianae* infesting *Solanum melongena* and *S. nigrum*. It was never recorded on tomato plants during the course of this survey but is a very active predator of *Raoiella indica* on coconut palms.

The life-history and bionomics, in Mauritius, of some of the more important predators have been studied and are given below.

Stethorus vinsoni.

The eggs are deposited singly on the under surface of the leaves; the number laid in one day varies from one to ten, the average being 3·5. Oviposition is intermittent during the adult life which has an average of 53·6 days; the mean number of eggs per female is 65·7.

The eggs are generally found close to a leaf vein, often underneath the web made by the Tetranychid mites. The egg is oval in shape and measures 0·30 mm. × 20 mm.; when freshly laid its surface is marked with hexagonal reticulations. It varies in colour from pale yellow to creamy white, and some 24–36 hours before the emergence of the young larva it becomes dark grey. The larva is light grey and turns to dark ash grey during succeeding moults. It starts feeding voraciously on the eggs and young stages of the mite soon after hatching.

The number of mites sucked and partially eaten in one day by a fully grown larva of *Stethorus* was 18·8 (average of 12 observations), the maximum eaten being 30. The average number of eggs eaten daily by one larva was found to be 40, 4 eggs being eaten in 50–60 seconds. A fully grown larva of *Stethorus* takes 6–8 minutes for feeding on an adult of *Tetranychus marianae*, the pumping and regurgitating process going on continuously during that time. The sucking of a young larva or nymph of the mite takes, on the average, 1½–2 minutes. There is a quiescent period of 12–24 hours before each moult. A fourth-stage larva measures from 2·2 to 2·9 mm. in length and 0·7 mm. in width. The number of *Stethorus* larvae on highly infested food-plants of the mite, mainly egg-plant, varies from 15 to 25 per leaf; on tomato plants, this number rarely exceeds 3–5 larvae per leaf.

The pupa, which measures 1·3 mm. × 0·9 mm., is attached by its posterior extremity to the under surface of the leaf. When newly formed it is reddish in colour, turning brown to greyish black later. The pupae are sometimes as numerous as the larvae.

The adult is of a shape typical of the genus *Stethorus*, black, clothed with fine hairs. For description, see Kapur (1948).

Copulation starts as soon as the adults hatch; the duration of this act lasts

TABLE VI.

Mean duration, in days, of various stages in the life-cycle of *Stethorus vinsoni* in summer (Oct.–Mar.) and winter (July–Sept.).

Stage	Summer (mean temperature 23 °C.)	Winter (mean temperature 18·2 °C.)
Egg	3	8
Larva : 1st stage ..	2	4
Larva : 2nd stage	2	4
Larva : 3rd stage	2½	6
Larva : 4th stage	4	7
Pupa	3½	5
Total : egg—adult	17	34

The prepupal stage lasts 12–24 hours in summer and 24–36 hours in winter.

from a few seconds to several hours. The pre-oviposition period is from 4–6 days. The number of mites eaten per day per adult beetle was found to be 16·2 (average of figures obtained for 10 adults, each kept in a tube 5 cm. × 0·75 cm.), the maximum being 42. Adults kept in these tubes and fed with mites lived for an average of 53·6 days, during which time a mean of 870 mites was eaten per beetle.

The average daily number of mite eggs eaten per beetle was 45 with a maximum of 90, one egg being eaten in 5–10 seconds.

Unfertilised females isolated in tubes laid eggs which hatched normally. The sex ratio of the resulting adults, as determined by dissection, was 109 males to 110 females.

Stethorus vinsoni is very often found in association with larvae of the Cecidomyiid, *Feltiella* sp. near *tetranychi*, on infested tomato and egg-plant in the field. On no occasion were larvae or adults of the former found preying on the latter.

The duration of the various stages as obtained from breeding in the laboratory is shown in Table VI, from which it is clear that the life-cycle of this Coccinellid is at all times of the year twice the length of that of the mite, *Tetranychus marianae* (Table II). This finding is in accordance with the field observations made during the last four years, namely that *Stethorus vinsoni* generally lags behind the mites in abundance and does not exert any beneficial effect until mite infestation has become more or less harmful to the plant attacked. The rôle of this Coccinellid as an effective enemy of mites is, therefore, very limited.

Feltiella sp. near *tetranychi*.

This Cecidomyiid, predatory in its larval form, attacks the eggs and young and adults of mites, particularly those of the various species of *Tetranychus*.

It lays its eggs singly on the underside of the leaves, sometimes on the web spun by the mites. The egg is oblong, pale yellow to white in colour and measures 0·18 mm. in length. On hatching, the young larva is of an amber colour and at once starts feeding; when fully grown it is reddish brown and measures 1·35–1·50 mm. in length and 0·35 mm. in width. It moves rather slowly in search of food and is often found in very large numbers on the lower surfaces of leaves of egg-plant and tomato. From 140 to 160 larvae, of all instars, are often

TABLE VII.

Mean duration, in days, of various stages in the life-cycle of *Feltiella* sp. near *tetranychi* in summer (Nov.–Jan.).

Stage	Summer (mean temp. 23·1 °C.)
Egg	1·5
Larva : 1st stage ..	2·5
Larva : 2nd stage ..	3·0
Larva : 3rd stage ..	4·5
Prepupa	1·5
Pupa	5·0
Total : egg—adult ..	18

found on a leaf of egg-plant with an area of about 152 sq. cm.; the mean number of larvae per leaf was 21. Larvae of the second and third stages consume daily from 9 to 12 eggs of *T. marianae* and an equal number of adult mites. A fully grown larva takes 5 to 8 minutes to suck an adult mite.

The cocoon is a compact oval white mass measuring about 0·8 mm. × 0·44 mm. It is rarely found in the field on the under surface of the leaf since larvae generally pupate in the soil. When kept in tubes, the larvae spin their cocoons in 24–36 hours. The pre-oviposition period varies from 2–3 days. When kept in tubes, adults live from 5 to 6 days if fed on dried raisins, but only 24 hours when kept without food. The duration of the life-cycle was obtained from laboratory rearings carried out in tubes (15 cm. × 3·5 cm.) provided at one end with a perforated cork fitted with very fine wire gauze and at the other with a layer of about 1·25 cm. of compressed and slightly moistened sphagnum moss. A piece of green leaf with eggs and mites of all stages was placed in the tube together with larvae and adults of the Cecidomyiid. Oviposition was obtained in a few cases in tubes. The number of mature eggs obtained on dissection of some females varied from 6 to 15; the maximum number of egg cells in the ovarioles was 35. The sex ratio from laboratory-reared individuals was 10 males to 56 females. The life-cycle of *Feltiella* sp. near *tetranychi* during the summer months of November–January (mean temp. 23·1°C.) is summarised in Table VII.

This predator is very rare in the field during the winter months of June to September; it is commonly associated with *Stethorus vinsoni* on plants heavily infested with *T. marianae*. Unlike that insect, the Cecidomyiid is as common on tomato as on other infested solanaceous plants, *viz.*: egg-plant, *Solanum nigrum*, etc. It is well distributed in all mite-infested centres and its incidence is at its peak when mite populations have reached a threatening density. Attacks of other members of the TETRANYCHIDAE, mainly *Oligonychus* spp., are sometimes checked by this predator. Heavy rainfall and violent gales affect the abundance and multiplication of *Feltiella* in the field.

Typhlodromus caudatus.

This mite ranks first as an important predator of the eggs of *Raoiella indica* on coconut. It has never been found preying on young stages or adults of this mite and was very seldom recorded attacking the various stages of *Tetranychus* spp.

The egg is oval, white to creamy white and measures 0·18 mm. in length and 0·14 mm. in maximum width; the larva on hatching is white and translucent but acquires a reddish tinge as soon as it has taken a first meal of eggs of *Raoiella*.

TABLE VIII.

Duration, in days, of various stages in the life-cycle of *Typhlodromus caudatus*.

Stage	February (mean temp. 24·3°C.)	July (mean temp. 18·0°C.)
Egg	1–2	4–6
Larva	1–2	2–4
Protonymph	1–2	2–3
Deutonymph	1–2	5–5
Total : egg to adult	4–8	13–18
Mean	6	15·5

Results are given of a survey of the predatory insects associated with the phytophagous mites. The most important predators on *Tetranychus* spp. are the Coccinellid, *Stethorus vinsoni* Kapur, and the Cecidomyiid, *Feltiella* sp. near *tetranychi* Rübs. The daily mite consumption of these predators is given. Other predators of secondary importance are *Oligota pallidicornis* Cam. and *Scolothrips* sp. near *indicus* Priesn.

The bionomics of *T. marianae* on tomato and of *Raoiella indica* on coconut were studied. Duration of the life-cycle of the former species varies from 4–9 days in summer to 15–22 days in winter. Twenty four to 30 generations of this species are estimated to occur in a year. *Raoiella* has a development period of 18–26 days from egg to adult in summer and of 30–36 days in winter.

A biological study of the predatory insects, *Stethorus vinsoni* and *Feltiella* sp., is given. Their beneficial effect is discussed. These two predators do not exert a control in time to check the build-up of the mite population. Their abundance is directly proportional to the incidence of the mite and the peak is generally only attained when the depredations of the latter have reached a disastrous level.

The various possible factors which have contributed to the sudden increase in the mite population on tomato during the last 6–8 years are discussed. Amongst the important factors are the following:—

(a) Absence of cyclonic disturbances with their heavy rains and violent gales which generally upset considerably the development of the mite population and reduce it to a minimum each year.

(b) Dressing of tomato and other vegetable crops with nitro-phosphatic fertilisers which were not applied until 10 years ago and which, it is thought, may have favoured an increase in the mite population.

(c) The abundance of natural reservoirs of wild food-plants that harbour *Tetranychus* spp. from which the subsequent spread results in the building up of mite colonies in cultivated areas.

(d) The ineffectiveness of *Stethorus vinsoni* as a predator on infested tomato plants.

Acknowledgements.

The author wishes to express his thanks to Dr. W. J. Hall, C.M.G., M.C., Director of the Commonwealth Institute of Entomology, for kindly transmitting the material collected to Dr. Owen Evans of the British Museum (Natural History) and to Mr. D. Macfarlane of the Commonwealth Institute of Entomology for identification. The ready co-operation of these gentlemen is acknowledged with gratitude. To Mr. R. Mamet the author is much indebted for his valuable criticisms in the preparation of the text.

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FIELD OBSERVATIONS ON ADULTS OF THE WHEAT BULB FLY (*LEPTOHYLEMYIA COARCTATA* (FALL.)).

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As a preliminary to the study of adult populations of Wheat Bulb Fly, *Leptohylemia coarctata* (Fall.), observations were begun in June, July and August 1953 by examining various crops on the Rothamsted Farm (fig. 1) for the presence of adults.

For several years an infestation had been known to exist in the continuous winter wheat on Broadbalk field. This experimental field, which consists of a

Fig. 1.—Plan of Rothamsted Experimental Farm.

number of long strips subjected to different manurial treatments, had been divided across its width in 1925 into five sections, one of which is kept bare fallow each year.* It has been generally recognised that, on heavy soils, egg-laying most readily occurs in bare fallows, so that the system of fallow followed by winter wheat on Broadbalk afforded an ideal site for the permanent establishment of Wheat Bulb Fly. The study of the fly populations was largely centred on this field and was begun in mid-June 1954. The plots chosen were those in section V (fig. 2) where wheat had followed a fallow and therefore constituted the chief emergence site for the field.

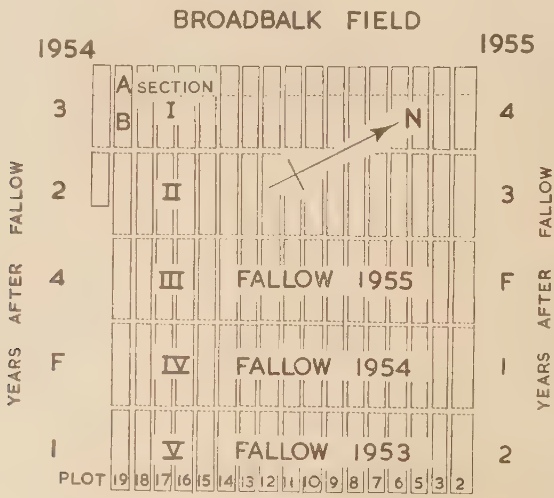

Fig. 2.—Plot and section plan of Broadbalk field showing system of fallowing.

Experimental Procedure.

A dual technique was employed of first catching, during a 30-minute period, the flies settled on the heads of wheat in an individual subplot and then uniformly

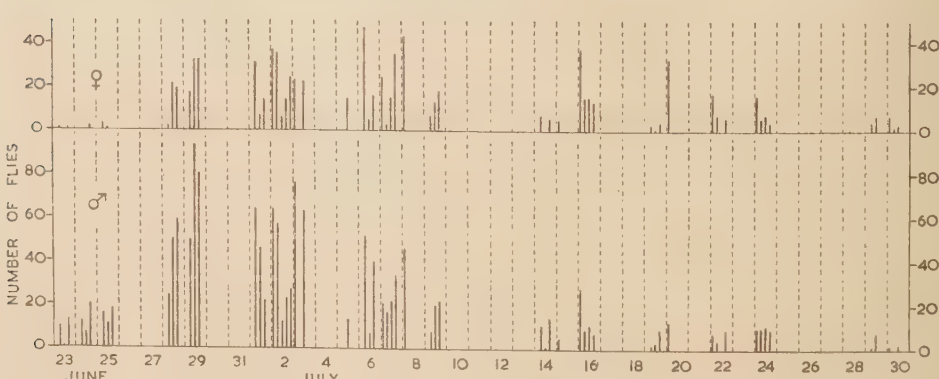

Fig. 3.—Numbers of flies occurring in the top catches in 1954. (For details see text.)

* Details of history and treatments are given in "Guide to the Experimental Farms" published by Rothamsted Experimental Station.

sweeping the same subplot with 25 standard sweeps made into the top 12 inches of the crop. An alternative dual technique was also used in which the 30-minute period of catching was replaced by 25 standard sweeps which just skimmed the top of the crop. These observations were generally carried out at one or more of the set times of 0530, 0830, 1230, 1630 and 1930 hr. (G.M.T.) during the day when records of temperature, humidity and windspeed and direction at crop height were taken. The results are given in figs. 3 and 4.

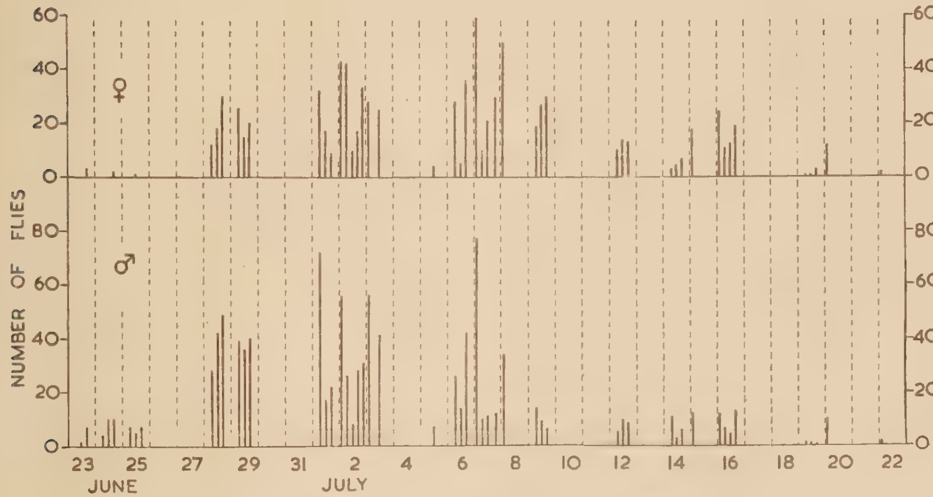

Fig. 4.—Numbers of flies occurring in the deep sweeps in 1954. (For details see text.)

Emergences and Life Span.

The survey of 1953 had shown that in late June and early July both males and females are abundant on Broadbalk. In 1954, the first males were caught on 21st June and the first females on 22nd June. In the observations on the subsequent population, the top catches gave results shown in fig. 5 which were very similar to those obtained by the deeper sweeping. Although in fig. 5 it is apparent that the emergence rate rapidly reached its peak, the emergence period was found to extend over the next 2–3 weeks, the last known freshly emerged male being taken on the 9th July and the last known freshly emerged female on the 14th July. In general, the males tended to emerge more simultaneously and to be slightly in advance of the females. In 1954, the males predominated during the peak emergence with a sex ratio of approximately 2:1. At this point in 1955, however, when the total numbers obtained daily was approximately one-tenth of those taken the previous year, the sex ratio was reversed, with the females exceeding the males in the ratio of 2:1.

The life span of the male was appreciably less than that of the female. In 1953, no males were found after the 3rd week in July, and in 1955, with a later general emergence, the last male was taken on the 29th July. In the cooler wetter summer of 1954, a few males were taken on 11th August, when they constituted 6 per cent. of the total. The females, however, generally persist in decreasing numbers till the end of August or the beginning of September. No comparable figures to show the end of the female life span have been obtained, due to the cessation of sweeping when the crop has been harvested in August.

These observations on the emergence, sex ratios and life span are supported by the quantitative study made by Dobson, Stephenson & Lofty (1958), in which these aspects are considered in greater detail.

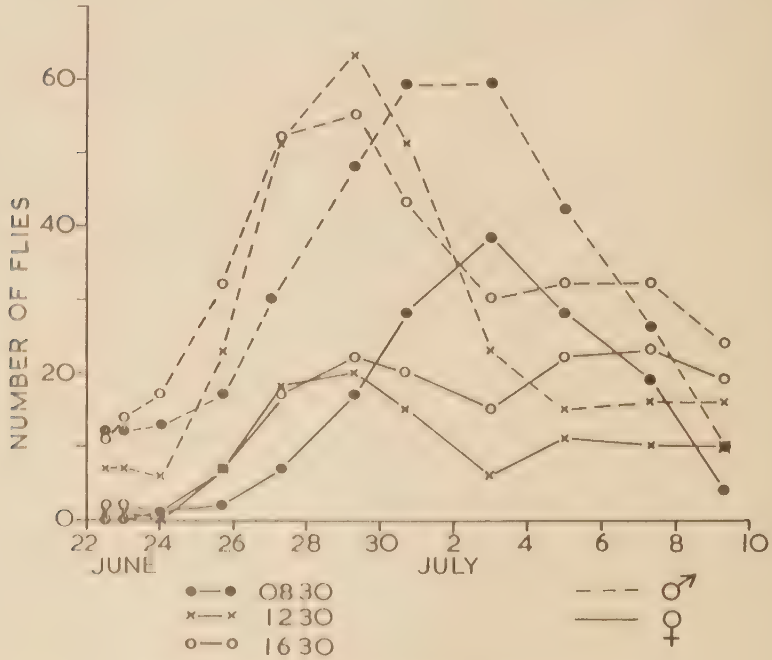

Fig. 5. Results of top catches showing population trends (three-day running means).

Diurnal Rhythms.

In 1954, it was observed that during the first week of the emergence period the numbers of flies being taken steadily increased throughout the day, as might be expected with a continual emergence. As the date of the population peak on the emergence site was passed, however, the diurnal pattern changed, with a rapid fall occurring in the numbers taken between 0530 and 1230, which was followed by a rise in the afternoon (fig. 6). After the end of the first week in July the pattern changed still further, with the greatest fall in the numbers taken occurring between 0530 and 0830, once again being followed by a rise in numbers after 1230. Since the afternoon build-up of numbers on the crop was found to continue after the end of the emergence period, this increase was considered to represent a general or localised return of the flies to the crop.

The appearance of this daily fluctuation in the numbers of flies on the crop raised a number of problems. What were the factors responsible for the fluctuation? Where did the flies go during the day, and did the increased numbers in the evening represent a general settling of an airborne population, or was there an active congregation on the wheat of the original or a mixed population? Does this phenomenon affect the eventual dispersion of the flies?

Observation showed that the initial drop in the numbers taken in the morning was due to increasing activity of the flies leading to aerial dispersion. A search of the wheat from the ground upwards both manually and using high-power

suction apparatus (Johnson, Southwood & Entwistle, 1957) failed to show any dispersion of the flies in the crop.

The dual technique used gave an indication of changes in activity by a comparison of the numbers caught on the heads of wheat with those of the sweeps applied deeper in the crop. Diurnal changes in activity, as shown by this method for the period 1st–20th July, are given in fig. 7, from which it can be seen that the results support the contention that activity increases in the morning and so leads to flight and aerial dispersion, whilst in the afternoon this activity subsides and the flies congregate once again on the crop.

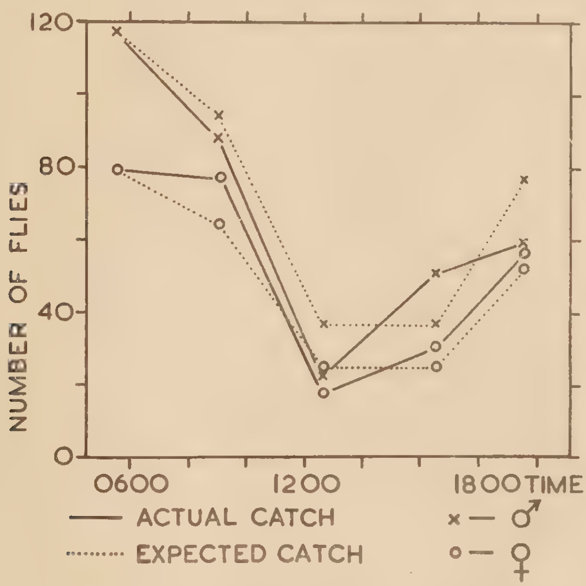

Fig. 6.—Variations in the numbers of flies caught throughout the day (2nd July 1954) and the variation in catch expected from the changes in temperature.

As might be expected, the largest numbers of flies were generally taken at 0530, before the flies which had settled the previous evening had become active and begun to disperse. The summer of 1954 was cool, and temperatures at this hour were often low, and it was observed that the temperature had to rise above 12–13°C. before the flight began. On each of 14 occasions of sampling after the initial emergence period, when the temperature had risen across this threshold for flight since the previous sample, the numbers taken decreased (Table I). Over the period of the whole day a partial regression of periodic samples with both wind and temperature showed that there was no correlation between wind and temperature or between windspeed and catch ($b = -0{\cdot}012 \pm 0{\cdot}025$). A strong negative correlation ($b = -0{\cdot}0918 \pm 0{\cdot}010$), however, was found to exist between the temperature and log catch (fig. 8).

The daily total of the numbers taken at 0830 hr. reached a peak at a later date than the coincident peaks for 1230 and 1630 hr. (fig. 5). This was most probably due to the fact that the temperature at 0830 did not rise above the threshold for flight between 28th June and 5th July. An inverse relationship between temperature and catch for 0830 is apparent in fig. 9, but the relationship for

1230 is more obscure and suggests that some other factor must have influenced the catch and be responsible for the catch curve obtained. The catch curve for 1630 also shows no clear inverse correlation with temperature, but the situation in the field appears to have been more dependent on that existing at 1230 hr.

The factors motivating the evening return to the crop have not yet been established, and, as has been pointed out, it seems unlikely that temperature alone is responsible. On 14 out of 27 occasions in 1954 and 1955, when the temperature at 1630 was greater than that at 1230, the number of flies obtained at 1630 still exceeded that at midday. It can be seen in fig. 6 that the midday catch was lower than that expected from the temperature difference with a fixed population, whilst the afternoon return was greater. In the warm summer of 1955, when high afternoon temperatures frequently persisted with only a slight fall till dusk, the evening build-up of numbers on the crop still occurred. Furthermore, the diurnal changes of activity indicated by the dual technique used in 1954 showed that in the case of the males the activity increased in the morning

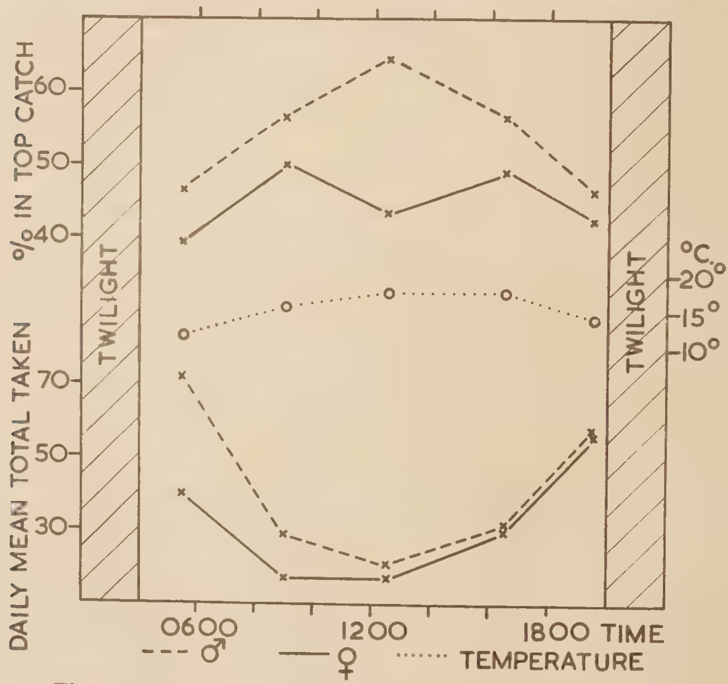

Fig. 7.—Mean changes of the population level occurring throughout the day during the period 1st–20th July 1954, showing changes in the level of activity as reflected by the percentage occurring in the top catch.

in step with the rise in temperature, but in the afternoon when little change of temperature was observed, it fell by a disproportionate amount whilst the numbers on the crop increased (fig. 7).

In the morning, as the temperature rose, the flies became increasingly active, but, in general, the males appeared to be the more active and tended to rest on the heads of wheat whilst the females remained deeper in the crop. This affected the percentage occurring in the top catches so that the value for the male was always greater than that for the female, as shown in fig. 7. Since the number

TABLE I.

Effect on numbers of flies taken in two consecutive catches, one made before and the other after a rise in temperature from a point below to one above the threshold for flight.

Below 13°C.	Above 13°C.
110	92
96	73
98	85
84	66
99	12
54	19
45	20
146	20
65	24
37	17
70	30
28	18
34	13
21	11

The catches were made, in 1954, after the end of the emergence period, so that the results are not influenced by the addition of newly emerged flies.

of flies on the crop at midday had remained minimal, the fall in the percentage in the top catch at 1230 for the females probably reflected a tendency to go deeper into the crop after alighting. Throughout the period of these observations an increasing tendency for the flies to return to the crop in the afternoon became most marked for the females in the first two weeks, after which it had remained well established until harvesting (fig. 9).

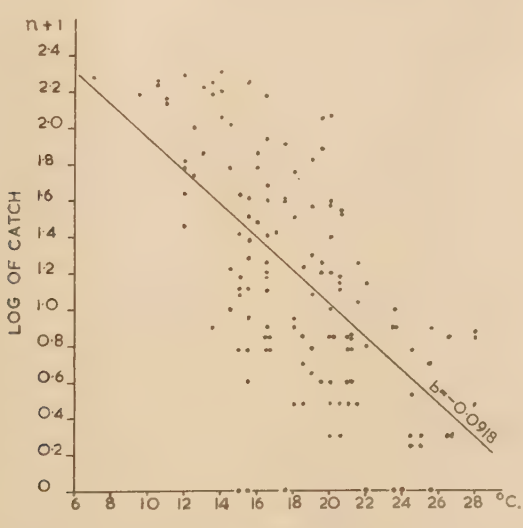

Fig. 8.—The relation between the log catch and the temperature.

Dispersion.

It was noted, in 1953, when sweeping for flies on various crops other than wheat in the vicinity of Broadbalk that few males were found. The females, however, whilst not as numerous as on the wheat in Broadbalk itself, were found on most sites examined. These included rye, barley, potatoes, sugar beet and wild vegetation growing in grass verges and in hedgerows. From this it may be

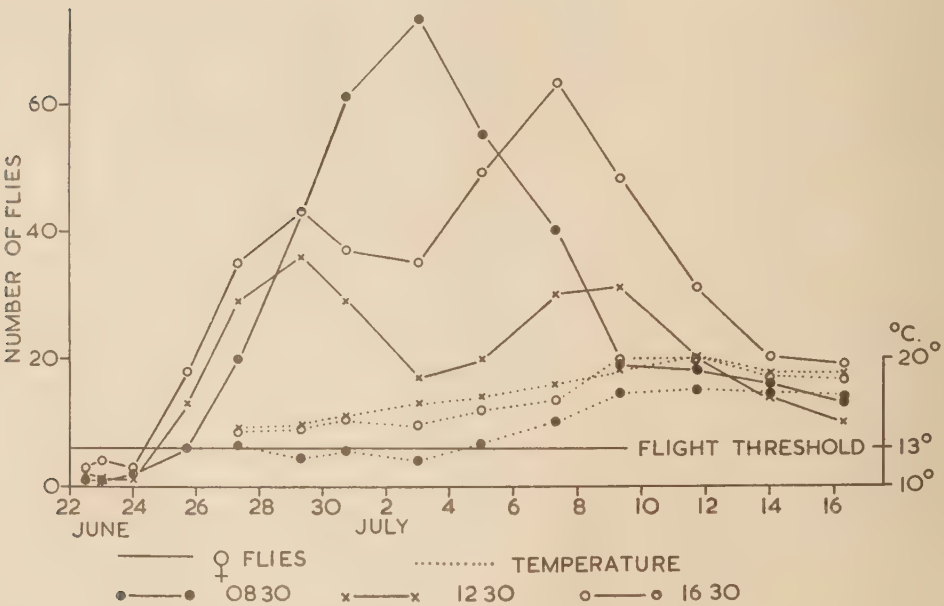

Fig. 9.—Variations in the total numbers (running means) of females taken at different times throughout the day in relation to temperature. (For details see text.)

concluded that at least in the case of the females there had been a general dispersion. However, it must be remembered that, apart from the main emergence section on Broadbalk, emergences would have occurred in the other wheat sections on Broadbalk, the Alternate Wheat and Fallow experiment and certain other rotation experiments which included winter wheat. Also from the work of Gemmill (1927), Gough (1946) and Stokes (1955) it is apparent that flies could have emerged from certain grasses growing by hedgerows and on strips of waste land surrounding the field. Under these conditions it is probable that at the time of emergence some flies were present throughout the whole area.

Release and recovery of radioactive flies.

To obtain more information on the nature of the dispersion of the flies from the emergence sites, 2,023 freshly captured flies comprising 823 males and 1,200 females which had been fed on sugar syrup containing ^{32}P and gave a minimum individual emission count of 600 per minute were released on plot 10^{V} of Broadbalk (fig. 2). To reduce radioactive surface contamination of these flies to a minimum and to encourage rapid feeding, the flies were fed in six-inch diameter glass cylinders fitted with wide-bore capillary feeding tubes suspended from the muslin cover (fig. 10).

The flies were released in two batches, on 7th and 20th July, respectively, each release being effected from a number of large containers placed uniformly round the outer margin of the wheat in plot 10 of section V, and only those flies which actively dispersed within a few moments after removal of the covers being included in the experiment, the remainder being removed with the containers. After capture, the labelled flies were released again on plot 10 of section V.

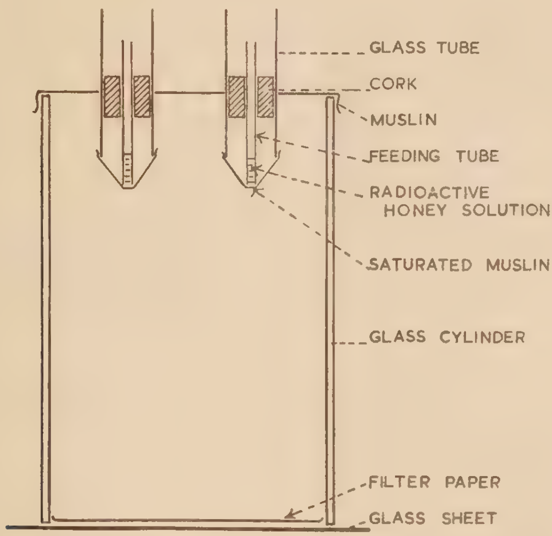

Fig. 10.—Cage for feeding large numbers of flies with radioactive solution.

Recaptures of labelled flies made after the first release are given in Table II. Following the second release, sweeping and collecting were carried out over a wider area.

From the results it was apparent that dispersion took place fairly rapidly and occasional recoveries were obtained from several of the plots in section V, covering practically the entire width of the field. No recoveries, however, were obtained from section III, on the other side of the fallowed section IV, but it should be pointed out that the total amount of sweeping in this section was appreciably less than that in section V. The last recapture was made shortly before harvesting on plot 2 of section V more than three weeks after the last, and five weeks after the first date of release of the marked flies, indicating that the same flies stayed in the area for an appreciable time.

An attempt to follow the pattern of immigration into an area was begun in 1954 shortly after the release of marked flies on Broadbalk. The site chosen was Long Hoos VII (see fig. 1), where no infestation had previously existed and spring wheat was being grown after sugar beet. Although in the course of the observations, flies, which must have been immigrants, were captured, no marked flies were recovered, but it is most probable that the immigrants came from one or other of nearer infestation centres existing in the Wheat and Fallow, 4-course and 6-course experiments.

From the results it was apparent that the population was declining on Long Hoos VII and that the immigration into the area had therefore occurred earlier. When comparing these results with those obtained earlier in the season from

Broadbalk, the rate of decline was found to be of a similar order and suggested that by the middle of July, when the earlier rapid fall in population on Broadbalk (see fig. 5) had changed to a slower steady rate, the population in the area, as represented by the female flies, had reached a fairly uniform level (fig. 11). The

TABLE II.

Recaptures from the first release of marked flies on Broadbalk field.

Date	Time since release (hours)	Plot	Total captures ♂♂	Total captures ♀♀	Percentage of captured flies radioactive ♂♂	Percentage of captured flies radioactive ♀♀
July 7	1½	10	27	13	14·8	0
	3½	10	33	34	3·0	3·0
	5½	10	85	96	8·2	7·3
	8	10	46	64	6·5	9·4
July 8	20½	10	78	93	15·4	11·8
July 9	48	10	31	47	3·2	2·1
	52	8	50	62	0	1·6
	56	8	30	87	0	3·4
July 12	120	16	0	0	0	0
		3	8	13	12·5	0
	124	16	0	0	0	0
		3	15	19	13·3	0
	128	10	0	0	0	0
		16	0	0	0	0
		3	10	13	10·0	0

The number of marked flies released uniformly round outer margin of plot 10v on 7th July 1954 was: ♂♂ 411, ♀♀ 490.

results also showed that males immigrated into the site, though probably to a lesser extent, for whereas they had outnumbered the females on Broadbalk, on Long Hoos VII they were outnumbered by the females by the order of 2:1.

The most reliable indication of the population decline was that given by the 0530 samples which showed for the females a reduction at the rate of 4 per cent. per day, whilst for the males it was 6 per cent.

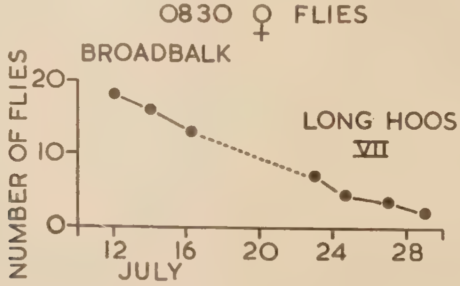

Fig. 11.—The mean numbers of female flies taken at 0830 hr. on Long Hoos VII during late July, together with the corresponding figures for an earlier period on Broadbalk.

Influence of light winds on distribution within the crop.

When sweeping Broadbalk (fig. 2) in 1954, it was noted that normal flight activity was not disturbed by breezes up to 8 m.p.h., and that flies congregated on the lee edge of each plot and appeared to be most numerous on those plots which constituted the lee edge of the entire field. However, during the period of sampling the prevailing wind was westerly so that section V generally formed the lee edge to the field and on only two occasions did the wind direction change sufficiently for section V to be slightly upwind. The contour of Broadbalk is such that there is a gentle fall in the level from section II towards section V. Under these conditions it was not possible fully to assess how far the movement of the flies was influenced by the wind or contour.

It had been noted that the greatest number of flies generally occurred in the NE. corner of Broadbalk affecting plots 2, 3 and 5 in section V which, with a prevailing west wind, was the most downwind area of the field. However, on 12th July, when a NNW. wind had been blowing for two days, thereby making the SE. corner the most downwind point, plots 3 and 16 of section V were sampled throughout the day and it was found that whereas plot 3 produced 45 males and 33 females, plot 16, which was the more downwind, only produced 22 males and 17 females.

On 16th July at 0530 hr., under conditions of a light westerly wind and a sub-flight temperature, the plots adjacent to plot 10 (section V) were sampled.

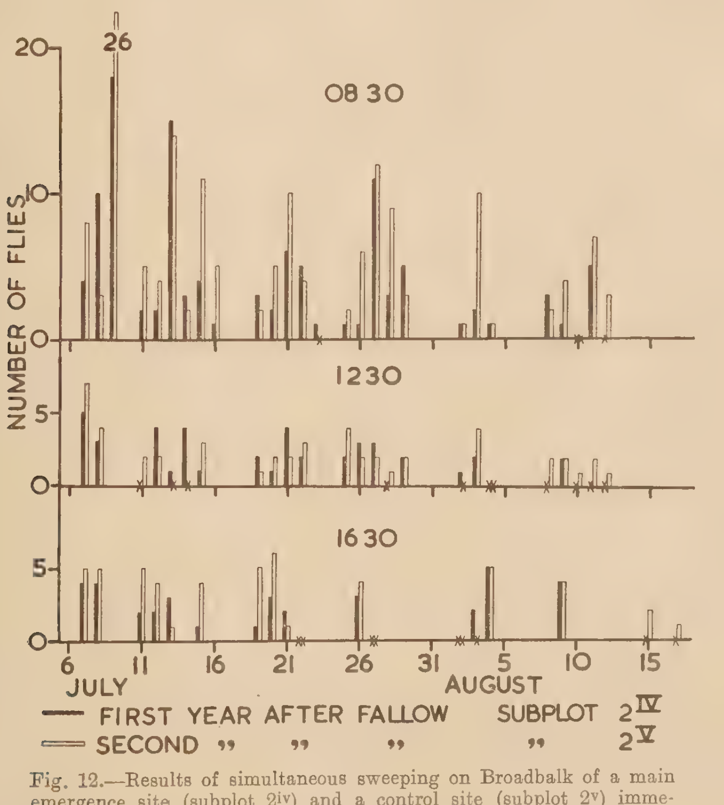

Fig. 12.—Results of simultaneous sweeping on Broadbalk of a main emergence site (subplot 2^{iv}) and a control site (subplot 2^{v}) immediately adjacent to it for the period 7th July to 12th August 1955. (For details see text.)

On 20th July at 0530 hr., under conditions of no wind and a sub-flight temperature, plot 10, section V, was sampled, together with plot 10 in sections I and III. It was noted that, whereas plot 10^{V} produced a similar result to that obtained on 16th July, it nevertheless yielded slightly more males and twice as many females as were obtained from plots 10^{I} and 10^{III}, the latter samples being nearly identical. However, throughout the previous day (19th July) the wind had been light and northerly and so had blown virtually across the field. This would suggest that wind was not the sole factor responsible for an uneven distribution on Broadbalk.

Distribution of flies within the crop in relation to emergence site.

In 1954 it had been noted that the greatest numbers of flies were to be found on section V when that section had been the chief emergence site. In 1955, however, section III was fallow and section IV being in its first year after fallow constituted the main emergence site so that by simultaneous observations on sections IV and V it was possible to determine the effect of the emergence site on the subsequent distribution of the flies.

Samples, each consisting of 50 standard sweeps, were taken from subplots 2^{IV} and 2^{V} at 0830, 1230 and 1630 hr. throughout the period from 7th July to 12th August (fig. 12). The daily totals for those days on which all three sets of sweepings took place are given in fig. 13. The daily decrease in the number of flies over the period for the subplots 2^{IV} and 2^{V} are shown by the regression lines ($b = -0{\cdot}33$, $P<0{\cdot}001$; $b = -0{\cdot}30$, $P<0{\cdot}001$). From the results it can be seen that the population on subplot 2^{V} was generally greater than that on the

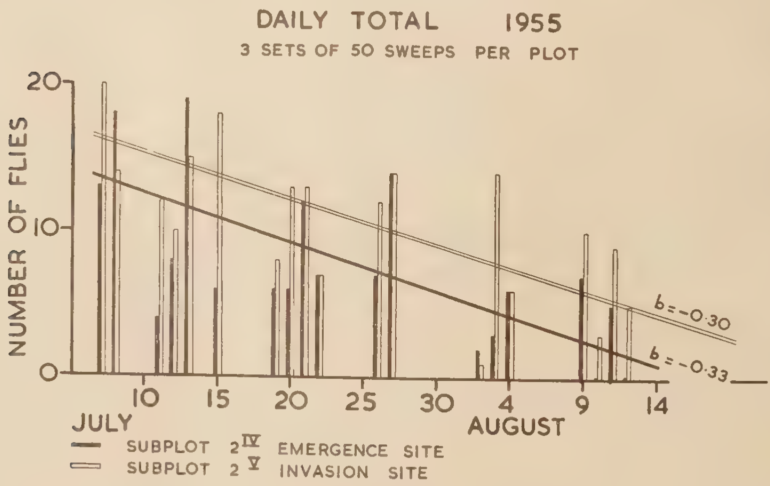

Fig. 13.—The relation between the emergence site and the dispersion of the subsequent population. (For details see text.)

emergence subplot 2^{IV} ($P<0{\cdot}05$). From this it may be concluded that the emergence site had no appreciable effect on the subsequent aggregation of flies on section V. Furthermore, the prevailing wind throughout the period was northerly and therefore blowing across the subplots being sampled, and not from one to the other. This would support the previous finding that the wind was not the primary factor responsible for the congregation of flies on section V.

In 1956, the centre section (III) of Broadbalk formed the chief emergence site for the field, and simultaneous sweepings of plots 2, 3, 10 and 19 in sections I,

III and V at intervals throughout the period from late June to early August (Table III) failed to show the aggregations observed in the previous two years on section V. During the earlier part of the period, presumably when the flies were still emerging, the greatest numbers were taken in section III, whilst the

TABLE III.

Mean numbers * of flies per set of sweeps taken on Broadbalk in 1956.

Males

Section		I				III				V			
Plots		2	3	10	19	2	3	10	19	2	3	10	19
June	27	—	—	—	—	12·5	11·6	—	—	4·0	4·0	—	—
	29	—	—	—	—	13·1	13·5	—	—	—	—	—	—
July	3	5·2	2·4	—	1·5	12·3	9·3	—	12·1	12·3	4·6	—	6·1
	6	—	—	—	—	13·5	12·2	—	—	—	—	—	—
(a.m.)	10	8·6	1·0	—	3·0	11·6	11·6	—	6·6	2·5	2·5	—	2·5
(p.m.)	10	11·7	3·1	—	12·9	12·6	11·9	—	12·0	5·5	2·2	—	12·8
	13	2·0	3·0	—	3·0	3·0	6·9	—	5·0	0	4·0	—	0·8
	16	—	—	—	—	14·2	12·3	—	—	11·6	1·5	—	—
	26	—	—	—	—	4·8	4·8	—	—	4·8	1·9	—	—
	27	3·8	—	2·5	3·7	11·8	5·7	11·6	6·4	12·4	—	12·2	12·3
Aug.	1	0	—	0·3	0	1·1	3·3	1·1	2·4	5·4	—	0	1·5
	3	1·0	—	1·0	3·0	—	—	—	6·6	—	—	—	5·4
	7	0	—	0	0·2	1·8	0	0·4	1·5	0	—	0	1·3

Females

Section		I				III				V			
Plots		2	3	10	19	2	3	10	19	2	3	10	19
June	27	—	—	—	—	11·6	5·8	—	—	5·3	1·5	—	—
	29	—	—	—	—	13·1	13·6	—	—	—	—	—	—
July	3	5·8	2·4	—	6·6	8·6	6·9	—	11·7	6·9	1·2	—	0·4
	6	—	—	—	—	12·8	11·9	—	—	—	—	—	—
(a.m.)	10	2·8	1·0	—	11·6	12·7	7·9	—	6·6	6·1	4·4	—	0·8
(p.m.)	10	12·6	11·9	—	12·0	6·1	5·4	—	12·0	5·5	8·8	—	7·1
	13	2·0	2·0	—	2·0	3·0	3·0	—	7·9	3·0	6·1	—	0
	16	—	—	—	—	13·6	12·8	—	—	12·7	12·5	—	—
	26	—	—	—	—	4·8	7·7	—	—	1·9	4·8	—	—
	27	12·0	—	13·2	12·9	12·8	12·7	13·2	12·2	12·0	—	13·3	11·9
Aug.	1	2·0	—	2·4	1·6	8·3	3·3	1·6	2·8	7·5	—	3·7	3·7
	3	7·9	—	6·1	11·7	—	—	—	12·2	—	—	—	12·5
	7	5·2	—	2·0	2·8	3·2	1·1	3·4	1·5	1·1	—	3·0	5·9

For details see text.

male and female dispersions over the field were similar. Later, however, the females dispersed more uniformly over the field whilst the males tended to congregate towards the lower end (fig. 14).

The influence of high winds on distribution within the crop.

In general, sweeping was only carried out when the mean windspeed was below 10 m.p.h. as experience had shown that with higher speeds, *e.g.*, 15 m.p.h., the flies settled deep in the crop close to the ground and their activity was

* Numbers corrected to 60°F.

restricted to crawling up and down the lower regions of the plants and flitting from stem to stem. In the case of higher mean windspeeds produced by strong gusts, sweeping carried out in the intervening lulls gave the impression that the distribution of the flies in the crop was not affected by the stronger winds.

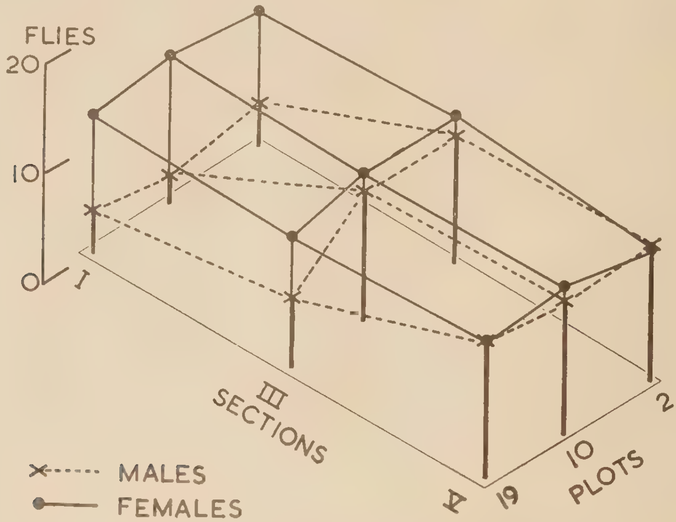

Fig. 14.—Population distribution on Broadbalk at 0545 hr. on 27th July 1956.

The effect of storms was clearly observed when studying the dispersion of the flies on Broadbalk in the cool, wet summer of 1956. The dispersion of the flies on Broadbalk at 0545 hr. on 27th July 1956 is shown in fig. 14. During 28th and 29th July, prolonged storms with southerly, gale-force winds swept the area. The dispersion for 0545 hr. on 1st August 1956, when similar weather conditions to those of 27th July prevailed, and it was again possible to carry out a set of simultaneous sweepings, is shown in fig. 15. It can be seen that the storms

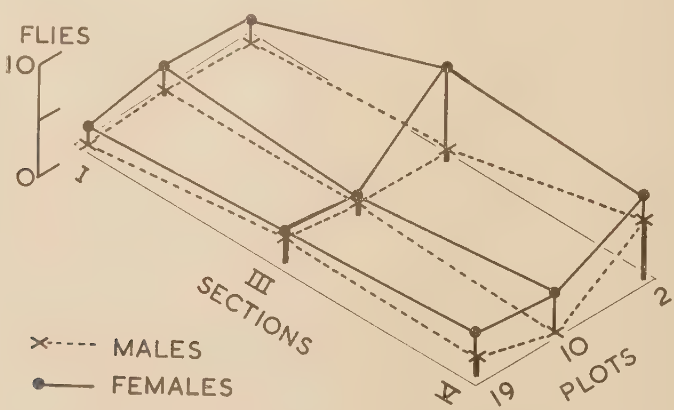

Fig. 15.—Population distribution on Broadbalk at 0545 hr. on 1st August 1956, after the storms of 28th and 29th July. (For details see text.)

moved the population towards the lee edge of the field, reducing the male population to less than one-fifth and the female population to less than one-third of their former levels. At this period, towards the end of the male life, the males appear to be more fragile and do not withstand handling as well as the females and no doubt this factor was partly responsible for the greater effect of the storm on the male population.

Sweeps carried out a week after the storm showed that the population had remained in its depleted state.

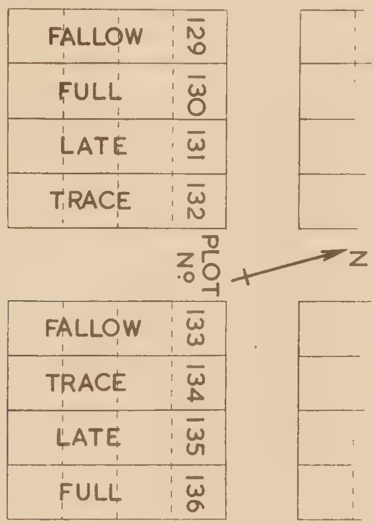

Fig. 16.—Arrangement of spring wheat plots in different states of flowering on Long Hoos VII.

The influence of flowering wheat on distribution.

The strips of wheat in the experiment of 1954 on Long Hoos VII (fig. 16), which is described in a later paper, flowered in a distinct sequence as the result of the treatment. When sampling was begun on this experiment in mid-July, two strips were in full flower, two were in late flower and two had only a trace of flower left. The results, which are given in Table IV, show that the females

TABLE IV.

Effect of flowering of wheat on fly congregation.
Mean no. of flies per sample.

Plots		130 + 136	131 + 135	132 + 134
Condition		Full flower	Late flower	Trace late flower
In flowering period (22–24 July)	♂♂	10·9	6·0	8·6
	♀♀	14·2	9·0	3·9
No. of observations		11	8	14
After flowering period (29–31 July)	♂♂	5·5	1·8	2·1
	♀♀	5·3	3·6	4·8
No. of observations		8	8	8

were particularly attracted to plots 130 and 136 whilst those plots were in flower but, when flowering was over, differences between the plots disappeared. The high value for the males obtained on plots 130 and 136 after flowering was due to aggregations, of the type described by Gough (1946), when in two samples a total of 34 flies was obtained. From these observations it may be concluded that the presence of flowering wheat can influence strongly the dispersion of the female fly whilst producing no marked effect on male dispersion.

Discussion.

In making a study of population movements the necessity for using a standard sampling technique is only too obvious. In these studies, sweeping with a hand net has been employed in the absence of a readily available better method. Sweeping, however, has many drawbacks, being subject to a number of variable external factors and only providing very limited information. A number of these factors has been discussed by DeLong (1932). When the heads of wheat are wet with dew the net becomes damp and heavy and its efficiency is impaired and so the net has to be changed repeatedly, and making a series of standard sweeps in rain is virtually impossible. This factor frequently upset the routine sweeping programme in the wet summers of 1954 and 1956. Furthermore, the standard sweep is only applicable to a particular type of crop and thereby precludes a quantitative determination of dispersal over other crops. Another difficulty is that of making simultaneous observations in a number of different sites. With sweeping, this involves a good supply of available labour, and even then the results are subject to variations between individuals. To obviate some of these difficulties, various trapping methods have been tried, using traps set at crop height. Water and bait traps with and without an attractant colour paint have proved completely unsuccessful. Sticky traps, too, proved ineffective though this may have been partly due to the size and the shape of the trap used. Somewhat better results were obtained with electric suction traps, but it was obvious that the 9-inch traps used were not nearly large enough, and the method could probably only prove of value when the population density was high. The exhaust of much larger traps, however, would flatten the surrounding wheat and so negate some of their value. The ideal solution still appears to lie in the production of an effective sticky trap or bait trap, together with high-level large suction traps to investigate aerial dispersion.

It has been shown that the diurnal flight rhythm, first observed in 1954 (pp. 80–81), was not simply due to the effect of the daily fluctuation of temperature on activity and it seems possible that light intensity may prove to be an auxiliary factor. When sweeping in the late evening there is often a distinct impression of a sudden increase in the number of flies on the crop in the half hour before dusk.

No direct information has so far been obtained on the nature of the daily flight activity. To regard this as a simple aerial dispersion over the crop would be to presuppose that the wheat site itself offered an adequate source of food for adult maturation. It has been observed that wheat when in flower can certainly influence the female dispersion four to five weeks after the initial emergence, and it seems probable that during an earlier period before fertilisation both males and females might equally be affected. In each of the three years of observation the wheat came into flower shortly after the beginning of the general emergence. The flower, however, lasts only about ten days, and whereas, apart from its flower, the wheat plant may afford a certain amount of food, this source alone does not appear to be adequate for complete development.* The daily dispersion, therefore, probably involves searching for food away from the crop before actively returning in the evening.

* From data not yet published.

The possible influence of searching for food on the dispersion could explain some of the differences observed between the males and females. Gough (1946) found that fertilisation of the females generally took place when the eggs were about half-developed, and three weeks after the maximum emergence, all the females examined had been fertilised. The demand for food is probably always greater for the female and would persist for most of her adult life, whereas the requirements of the male would probably be relatively small after maturation. Thus the tendency of the female to go deeper into the crop and to disperse more widely from the emergence fields might well reflect differences in the food requirements and feeding habits of the two sexes.

It had been noted when sweeping that breezes of up to 8 m.p.h. did not appear to upset the normal flight activity but winds of 15 m.p.h. sharply reduced free flight whilst they did not appear to influence materially the distribution of the flies. The opportunity to observe the effects of stronger winds did not arise in 1954 or 1955 so that the depletion by storms of the population on Broadbalk observed in 1956 was of singular interest as it indicated that the flies could be blown out of the area and were not, in this case, effectively replaced by other flies blown into it, the population thereafter remaining depleted. Bearing in mind the tendency of the Wheat Bulb Fly to aggregate on wheat fields, this would suggest that the extent of the original dispersion was not very great and that a series of more or less localised populations may be set up round infested fields. This view would appear to be further supported by the finding that marked flies remained in the vicinity of their point of release for considerable periods. Furthermore, other observations have shown that within an infested field the dispersion may not be uniform, appreciably greater numbers of flies occurring in some regions than in others. Concentrations of this nature would be likely to lead to localised regions of heavy egg-laying in their proximity and so affect the overall pattern of the next infestation. A greater knowledge of the extent of the dispersion and the factors which influence it could prove of material assistance in forecasting areas of potentially high infestation and so permit a form of natural control by crop-site planning.

Summary.

A study of adult populations of Wheat Bulb Fly, *Leptohylemyia coarctata* (Fall.), has been carried out in the field by routine sweeping at Rothamsted. It has been observed that the males emerge slightly before the females and that the emergence period may cover at least three weeks in late June and early July. Although the number of males may exceed the number of females at first, the females predominate later in the season due to the shorter life span of the males.

The numbers of flies on the wheat have been found to fluctuate appreciably throughout the day. During the first week of the emergence period the number of flies taken increased steadily throughout the day. After the date of population peak, however, the maximum numbers occurred in the crop in the very early morning and the late evening, which suggested a daily flight dispersion followed by a general or localised return of the flies to the crop. Further study of the data showed that the daily temperature rhythm was only partly responsible for this daily flight dispersion, and that there appeared to be an active return flight to the crop in the evening. Generally the males were more active than the females and did not settle so deeply in the crop.

The temperature threshold for flight was observed to be 12 to 13°C. Winds up to 8 m.p.h. did not appear to affect flight activity, but higher winds, *e.g.*, 15 m.p.h., markedly reduced flight, the flies remaining deep in the crop near ground level. Gale-force winds, however, were observed to produce a permanent

depletion in the number of flies infesting Broadbalk field, indicating that the population was probably localised.

Although portions of the populations dispersed fairly rapidly from the emergence sites, recaptures of radioactive flies labelled with ^{32}P indicated that the extent of the dispersions was not very great. The females dispersed more than the males, and were influenced to some extent by the occurrence of wheat in flower. Frequently the flies were found to have congregated on the lee edge of the crop, but other preferred regions have been observed which could not be attributed to the influence of the wind.

Acknowledgements.

I wish to express to Dr. K. Mellanby my appreciation of his kindness in reading this manuscript and to Miss J. Young of Durham University and Mr. R. Stoltz of Nottingham University and others of their assistance with routine crop sweeping.

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A QUANTITATIVE STUDY OF A POPULATION OF WHEAT BULB FLY, *LEPTOHYLEMYIA COARCTATA* (FALL.), IN THE FIELD.

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(Plate II.)

Extensive studies of adult populations of Wheat Bulb Fly, *Leptohylemyia coarctata* (Fall.), in Britain were carried out by Gough (1946) using a standardised sweeping technique. Irregularities of distribution suggested considerably differing habits and activities of the sexes, but the data could not be fully explained as the numbers caught depended both on the size of the population and on the degree of activity of its members at the time. This difficulty in evaluating data obtained by sweeping alone has also been pointed out by Long (1958). Clearly, knowledge of the absolute sizes and compositions of the populations would have assisted interpretation of these data.

The main purpose of the present work was to estimate the absolute numbers of flies of each sex and of every age present in a natural population during the whole period of adult life. Some observations on immature stages were also made so that natural mortality from egg to imago could be estimated.

The work was carried out during 1956 at Rothamsted, on Pennell's Piece, a small area of land adjoining the classical wheat field, Broadbalk. The soil type of Pennell's Piece is a heavy loam derived from the geological deposit " clay with flints ".

After lying fallow for two years, the site had been sown during autumn 1955 with wheat (variety Cappelle) at the rate of two bushels per acre. Preliminary inspection during the spring of 1956 showed that this wheat was moderately infested.

Methods.

The work consisted principally of a study of the development and decline of a population of adult flies. This was supplemented by observations on the populations of the immature stages.

To study emergence, a large cage of terylene netting, 24 ft. long, 12 ft. wide and 6 ft. high, was used (Pl. II, figs. 1 & 2). It was erected over a plot of infested wheat in mid-June shortly before the flies were expected to appear and was searched twice daily, at approximately 10–11 a.m. and shortly before sunset. To avoid unnecessary damage to the plants, paths were cut through the wheat. Full details of the construction of the cage and of the effect it had on the climate of the enclosed area are given in the Appendix.

In order to find the flies, the wheat was gently beaten by hand. This caused many of them to fly up to the walls and roof of the cage where they could easily be captured with a mouth-suction apparatus (Poos, 1929). After this the soil surface and plants were searched but very few additional flies were found. Searching usually took about an hour but was always continued until it seemed unlikely that any more flies would appear.

Population decrease was investigated by the method of marking, releasing and recapturing. Every day the newly emerged flies caught in the cage were removed to the laboratory, and after light anaesthetisation by chilling (six minutes

in a tube placed in a refrigerator at $-5°C$.) were marked with either one spot or two spots of Artist's oil colour applied to the dorsum of the thorax with the head of a fine pin. The colour or combination of colours was changed daily so that the marks indicated dates of emergence. After being marked, the flies were immediately returned to the cage.

A search for marked flies was made on every third day during the morning search for unmarked ones and the numbers, marks and sexes of those captured were recorded. The flies were then released again. Marked flies were sufficiently conspicuous to make it possible to avoid capturing them except when required. Searches were carried out regularly until 4th September, nine days after the last flies had been seen.

Effects of Anaesthetisation and Marking.

Although flies appeared to recover quickly after marking, there were frequently large differences between the numbers of newly marked flies released in the cage and the corrected * numbers recaptured for the first time. This difference was greater for flies marked with two spots of paint than for those marked with one spot; of 143 males with one spot, 60·3 per cent. were known to be alive on the day after marking and, of 150 males with two spots, 46·5 per cent. were alive. The corresponding figures for females were 78·4 per cent. of 47 with one spot and 58·7 per cent. out of 211 with two spots. It seems likely from the above figures that the initial loss was due to the harmful effect of marking.

A laboratory experiment was therefore carried out to test the effects of marking and anaesthetisation on the length of life of Wheat Bulb Fly. Neither treatment appeared to have any effect, and all groups survived equally well. However, the flies used in this experiment differed from those marked and released in the cage in that having been obtained by general field collecting they were of mixed ages whereas the latter were all newly emerged.

It was not possible to repeat the laboratory experiments using newly emerged flies, but there is evidence from the literature that very young insects are frequently less robust than older ones. Jackson (1948) found that marking with oil paints appeared to be more harmful to newly emerged tsetse flies than to older ones, and insecticide workers have frequently found very young insects to be relatively highly susceptible to toxic substances (Morrison, 1943; Mukerjea, 1953; Craufurd-Benson, 1938; Kerr, 1954). There are grounds therefore for believing that the initial losses in the cage were due to marking.

It is equally important to know whether the length of life of marked flies which did not die shortly after marking was affected. Again, this could not be tested directly with newly emerged flies but there is reason for supposing that there was no appreciable effect. In the field cage there was no apparent difference in the survival rate of flies which had survived the initial loss whether they were marked with one spot of paint or with two, and, in the laboratory experiment, marked and unmarked flies survived equally well. In support it may be noted that Jackson (1952, p. 16) found that there was no difference in survival between marked and unmarked groups of tsetse flies over the six weeks following that of release.

The nature of this supposed marking effect is unknown. None of the paints contained poisonous pigments, but the solvent, which tended to spread and leave a permanently blackened area, may have been toxic. It is unlikely that the weight of the paint (approximately 0·5 mg. per spot) was of importance as, although it amounted to between 5 and 12 per cent. of that of the flies, there were no differences in length of life between individuals marked with one spot and those marked with two.

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* This is explained later on p. 102.

TABLE I.

Marking and recapture data for male flies.

Date	No. emerged	No. of days after marking	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
			Numbers of flies recaptured																																
June 24	4				1			1			2			0			0			0			0			0			0			0			0
25	3			1			0			0			0			0			0			0			0			0			0			0	
26	8		3			1			5			1			0			0			0			0			0			0			0		
27	10				7			3			1			0			0			0			0			0			0			0			0
28	10			8			6			4			2			3			2			1			0			0			0			0	
29	12		4			4			2			2			3			3			4			2			0			0			0		
30	13				1			1			2			0			1			1			0			0			0			0			0
July 1	30			21			9			4			3			7			3			4			1			1			0			0	
2	26		12			14			9			9			7			6			5			4			1			0			0		
3	27				10			7			9			6			5			1			2			1			0			0			0
4	32			21			12			6			5			6			4			3			4			2			1			0	
5	31		14			5			7			6			2			2			2			2			1			1			0		
6	40				14			15			14			9			6			4			2			4			0			1			0
7	9			0			5			5			2			0			0			0			0			0			0			0	
8	4		0			2			0			0			0			0			0			0			0			0			0		
9	3				0			0			0			0			0			0			0			0			0			0			0
10	2			0			0			0			0			0			0			0			0			0			0			0	
11	2		1			0			1			1			1			1			0			0			0			0			0		
12	4				0			0			0			0			0			0			0			0			0			0			0
13	1			1			1			1			0			0			0			0			0			0			0			0	
14	2		0			0			0			0			0			0			0			0			0			0			0		
15	11				6			5			4			1			0			0			0			0			0			0			0
16	4			2			0			0			0			0			0			0			0			0			0			0	
17	4		3			0			1			0			0			0			0			0			0			0			0		
18	0				0			0			0			0			0			0			0			0			0			0			0
19	1			0			0			1			0			0			0			0			0			0			0			0	

TABLE II.

Marking and recapture data for female flies.

Date	No. emerged	No. of days after marking	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
			Numbers of flies recaptured																									
June 21	1				1			1			1			1			1			1			0			0		
22	0			0			0			0			0			0			0			0			0			0
23	0		0			0			0			0			0			0			0			0			0	
24	1				0			0			1			1			0			0			0			0		
25	2			1			0			0			0			0			0			0			0			0
26	2		2			1			2			0			0			0			0			0			0	
27	2				2			0			0			0			0			0			0			0		
28	2			2			1			2			0			0			0			0			0			0
29	5		3			1			3			3			2			3			3			3			2	
30	2				0			0			0			0			1			1			0			2		
July 1	10			6			2			1			1			0			0			0			0			0
2	10		5			6			4			4			5			5			3			2			3	
3	10				3			4			3			1			2			2			2			2		
4	11			4			6			5			5			5			4			3			2			2
5	11		2			4			6			3			3			1			3			1			0	
6	29				14			13			8			9			6			6			5			4		
7	35			4			4			9			10			9			9			6			4			3
8	37		15			24			20			19			13			9			5			2			3	
9	17				4			5			1			1			2			1			4			1		
10	17			13			8			10			6			6			5			3			4			3
11	8		4			4			4			2			1			0			0			0			0	
12	2				0			0			0			0			0			0			0			0		
13	4			2			3			2			2			3			3			1			1			1
14	0		0			0			0			0			0			0			0			0			0	
15	3				1			0			0			0			0			0			0			0		
16	7			7			2			3			3			3			2			3			1			1
17	4		1			0			2			0			1			1			0			0			0	
18	6				4			5			2			1			1			1			1			1		
19	10			0			0			1			0			0			0			0			0			0
20	2		0			1			1			1			0			0			0			0			0	
21	4				1			2			0			1			3			3			1			0		
22	1			0			1			0			0			0			0			0			0			0
23	1		0			0			0			0			0			0			0			0			0	
24	1				0			0			0			0			0			0			0			0		
25	1			0			0			0			0			0			0			0			0			0

TABLE II—*continued.*

Marking and recapture data for female flies.

Date	No. emerged	No. of days after marking	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
			Numbers of flies recaptured																								
June 21	1		0			0			0			0			0			0			0			0			0
22	0				0			0			0			0			0			0			0			0	
23	0			0			0			0			0			0			0			0			0		
24	1		0			0			0			0			0			0			0			0			0
25	2				0			0			0			0			0			0			0			0	
26	2			0			0			0			0			0			0			0			0		
27	2		0			0			0			0			0			0			0			0			0
28	2				0			0			0			0			0			0			0			0	
29	5			2			0			0			0			0			0			0			0		
30	2		2			0			0			0			0			0			0			0			0
July 1	10				1			0			0			0			0			0			0			0	
2	10			3			1			1			1			0			0			0			0		
3	10		0			0			0			0			0			0			0			0			0
4	11				1			1			1			1			1			1			1			1	
5	11			0			0			0			0			0			0			0			0		
6	29		3			0			1			1			0			0			0			0			0
7	35				3			1			1			1			1			1			1			1	
8	37			2			1			2			0			0			0			0			0		
9	17		0			0			0			0			0			0			0			0			0
10	17				4			4			4			3			0			0			0			0	
11	8			1			2			0			0			0			0			0			0		
12	2		0			0			0			0			0			0			0			0			0
13	4				0			0			0			0			0			0			0			0	
14	0			0			0			0			0			0			0			0			0		
15	3		0			0			0			0			0			0			0			0			0
16	7				1			0			0			0			0			0			0			0	
17	4			0			0			0			0			0			0			0			0		
18	6		0			0			0			0			0			0			0			0			
19	10				0			0			0			0			0			0			0				
20	2			0			0			0			0			0			0			0					
21	4		0			0			0			0			0			0			0						
22	1				0			0			0			0			0			0							
23	1			0			0			0			0			0			0								
24	1		0			0			0			0			0			0									
25	1				0			0			0			0			0										

Results.

Flies were first seen in the field outside the cage on 20th June, and the first was caught inside on 21st June. From that date, regular collections were made and searching was continued until 4th September, nine days after the last fly had been seen. The entire data for male and female flies are shown in Tables I and II, respectively. The first entry of each line shows the number of flies originally marked, and the succeeding entries the numbers recaptured on successive days. The numbers caught showed a sharp reduction between the first capture and first recapture and thereafter a gradual fall until no more flies were caught.

The proportion of the total population captured each day depended both on the activity of the flies and on the efficiency of the searching technique. Deficiencies amongst newly emerged flies were minimised by carrying out two searches a day, and amongst recaptured flies by correction of the data.

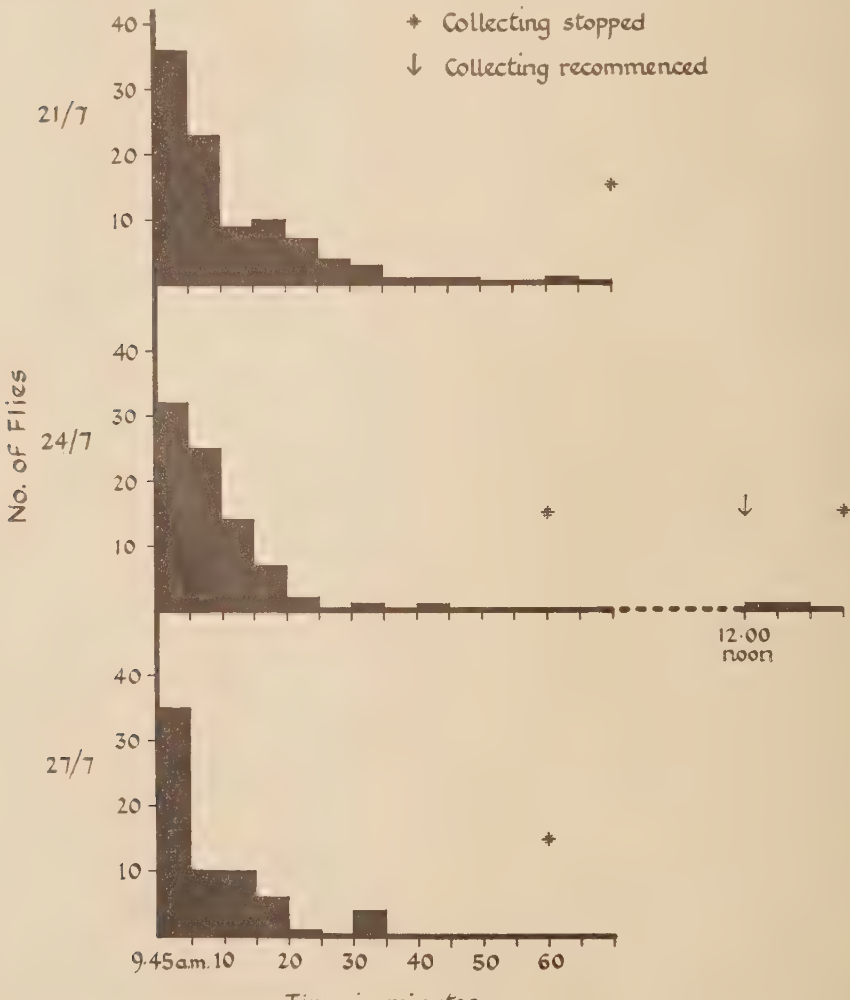

Fig. 1.—The numbers of *L. coarctata* caught at five-minute intervals during the mornings of three separate days.

The technique was tested by carrying out timed collections of at least an hour's duration on 21st, 24th and 27th July. On each date, most of the flies were caught during the early part of the search; after half an hour over 90 per cent. of the final total had been caught, and after 45 minutes only isolated individuals were found (fig. 1). On 24th July a second search, of 15 minutes' duration, carried out $1\frac{1}{4}$ hours after finishing the first, revealed only two more flies. It is thought, therefore, that losses due to inefficient searching were not serious. Further evidence of this was afforded by the constant reappearance of several flies which could be recognised individually, *e.g.*, the female first captured on 21st June was seen 23 times in 25 successive searches before it disappeared finally, and two females first captured on 28th June were both seen in seven out of ten searches, and one of them was seen on two of the remaining occasions.

Errors due to differences of activity, although partly compensated by thorough searching, could not be completely avoided. Their effect could however be minimised by the statistical treatment.

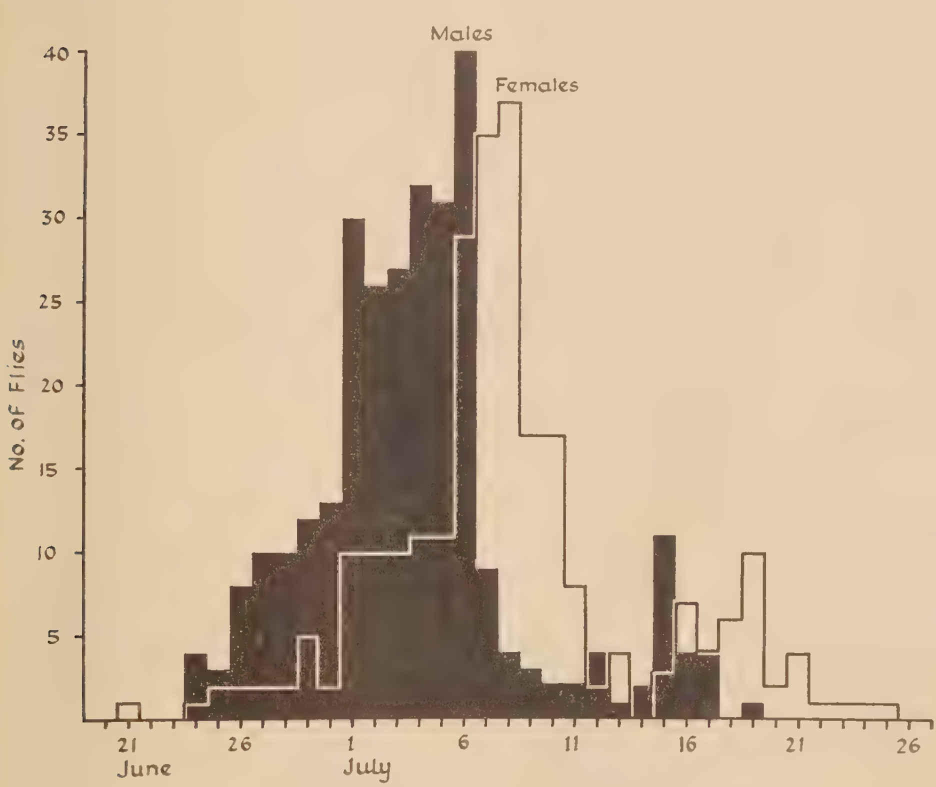

Fig. 2.—The daily emergence figures for males and females of *L. coarctata* in the cage.

Emergence pattern.

The first entries in each line of Tables I and II show the daily emergence figures for males and females. These are illustrated as day to day frequency diagrams in fig. 2 to show the emergence pattern.

Male flies were first seen on 24th June. After this, apart from temporary checks, the daily catch of males increased, reaching a maximum of 40 flies on

6th July. The catches then decreased, and apart from a sharp increase on 15th July remained low until the last freshly emerged fly was caught on 19th July. In all, 293 males were caught during 26 days, and of these, 186 (63%) emerged between 1st and 6th July. This period of six days may therefore be termed the "period of maximum emergence". The highest single day's catch occurred at the mid-point of the emergence period, but the distribution of values around this was markedly asymmetrical, 206 flies (70%) occurring in the period before it, and only 47 (16%) occurring in the period after it.

The first female was found on 21st June, but very few appeared until 1st July when there was a sharp increase. Remaining steady for the next few days, the catch increased again on 6th July and reached a maximum of 37 flies on 8th July. Thereafter there was a rapid decrease, and except for a small increase between 16th and 19th July, numbers remained low until the last freshly emerged fly was caught on 25th July. In all, 258 females were caught during 35 days, and the period of maximum emergence, during which 135 flies (52%) were caught, was from 6th to 10th July inclusive. As with the males, the highest catch occurred at the mid-point of the emergence season and the distribution was asymmetrical, 133 flies (52%) being caught before the maximum and 88 (34%) after it.

The emergence patterns of the sexes, although similar in general form, differed in timing and in degree of asymmetry. The maximum emergence period of the male pre-dated that of the female by some five days, and a greater proportion of the males emerged before the mid-point of the emergence season. Female emergence also spread over a longer period than that of the males. The small increases in the daily emergence figures which occurred in both sexes about a week after the period of maximum emergence are of interest. They suggest that at some stage of development a small portion of the population may have been delayed and that this delay had persisted. This division of the population was also evident amongst the larvae on 31st May when, except for a small minority which were still in their second instar, most had completed their growth and had left the plants.

The check to the rising daily catches of both sexes which occurred between 2nd and 5th July is also of interest. The reason for this is not known, but as it occurred in both sexes simultaneously it may have been the result of some event about the time of emergence.

The final totals, 293 males and 258 females, were sufficiently close to suggest that the sexes are fundamentally equal in numbers.

Population decline.

Rate of population decline was estimated from recapture figures of marked flies. The number of recaptures depended partly on the activity of the flies and partly on the efficiency of searching, so that sometimes not all the flies subsequently found to be alive were captured. Errors due to this were reduced by correcting the figures to show the numbers known to be alive on each day rather than the numbers actually recaptured. For example, the values for male flies marked on 5th July before and after correction are as follows:—

Date	July 5	6	9	12	15	18	21	24	27	30
Uncorrected	11	2	4	6	3	3	1	3	1	0
Corrected	11	6	6	6	3	3	3	3	1	0

When summed for all dates and expressed as percentages of the numbers marked, the corrected recapture figures show that there was a heavy loss of flies during the first day followed by a gradual decrease in numbers. As this high initial loss was believed to be due to marking, the rate of population decline was estimated from corrected recapture figures alone, that is, without reference to the original numbers marked. If the gradual decrease is due solely to random

mortality, then the number of flies will decrease logarithmically with time, that is, there will be a straight-line relationship of the form " y = a − bx " where " y " is the logarithm of the numbers of flies, and " x " is the number of days after marking. The slope of the line, " b ", estimates the rate of decrease and is independent of the intercept at the " y " axis, " a ",—the estimated logarithm of the number of flies at the start. Comparison of the antilogarithm of " a " with the number marked enables the size of the initial loss to be estimated.

The data were insufficient for each day's emergence to be dealt with separately, so a mean rate of decrease based on the entire data for each sex was calculated. As observations were made every three days, the data fell into three groups, depending on whether observations started one, two or three days after marking. Taking each group separately, the logarithm of the summed corrected recaptures was plotted against time. In each case the points at first fell approximately on a straight line but later, as the numbers of flies decreased, they became erratic. In calculating the regression lines, therefore, only points based on ten or more flies were used. The group regressions were used to estimate initial mortality, but to estimate rate of population decrease they were combined into a common regression. From this the half-life of the population could be calculated, and was estimated to be 7·3 days for males and 11·1 days for females. The equations and deductions from them are shown in Table III. (The data for males were more variable than those for females and the slopes of the lines differed significantly—variance ratio, 2/12 d.f., 4·2. It is not thought however that the use of the common regression in this case was misleading.)

Population size and composition.

As the regression coefficients expressing rates of population decrease are independent of the numbers of individuals in the population, they can be applied to the daily emergence figures to estimate the numbers of flies left after any period of time. This enables a general picture to be obtained of the size and composition of the population at any time during the period of adult life.

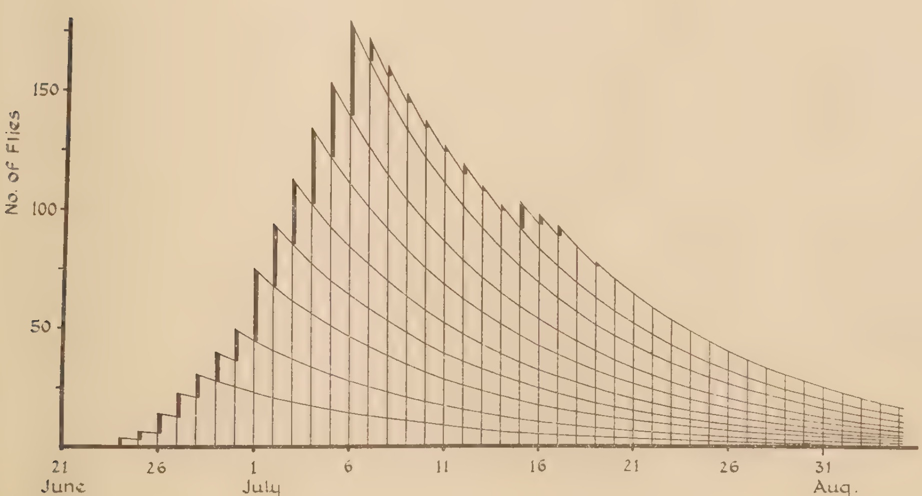

Fig. 3.—The theoretical structure of the male population of *L. coarctata* in the cage.

TABLE III.

Analysis of recapture data.

Sex	Group	Regressions*	Nos. marked		Estimated nos. surviving 1 day		% deaths through marking**	Common regression	Half-life of population
Females	1, 4, 7, etc., days after marking	y = 1·80 − 0·031x	81		63				
	2, 5, 8, etc., days after marking	y = 1·75 − 0·025x	100	258	56	165	36	y = 1·74 − 0·27x	11·1 days
	3, 6, 9, etc., days after marking	y = 1·66 − 0·025x	77		46				
Males	1, 4, 7, etc., days after marking	y = 1·66 − 0·034x	89		46				
	2, 5, 8, etc., days after marking	y = 1·81 − 0·048x	92	293	65	182	38	y = 1·75 − 0·04x	7·3 days
	3, 6, 9, etc., days after marking	y = 1·85 − 0·049x	112		71				

* y = log no. flies.
x = No. days after marking.
** Pooled for flies marked with one spot and with two spots. The proportion of females marked with two spots was higher than that of males.

The reconstructed populations for males and females, respectively, are shown in figs. 3 and 4. The figures show for each day:

(1) The total number of flies (heights of vertical lines).
(2) The number of new emergences (thickened portions of vertical lines).
(3) The number of flies of each age (portions of vertical lines between successive converging curves).

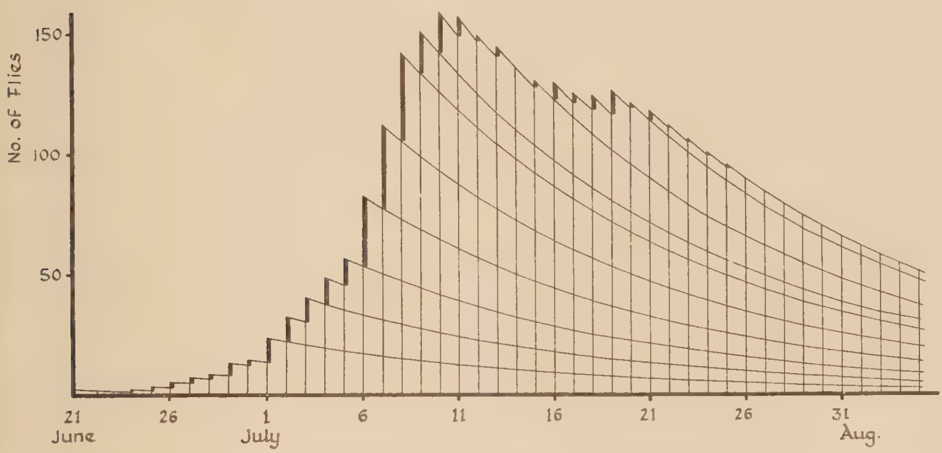

Fig. 4.—The theoretical structure of the female population of *L. coarctata* in the cage.

Populations of males and females showed similar trends (fig. 5). There was a rapid increase in total numbers to a sharp maximum and then a more gradual decrease. The male maximum (179 flies) occurred on 6th July and the female (159 flies) on 10th July. From 24th June until 8th July males were predominant

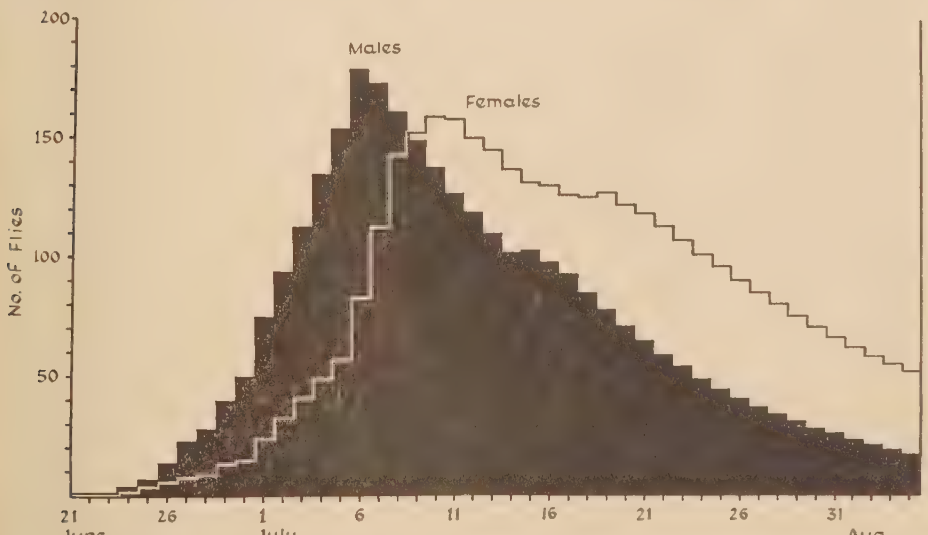

Fig. 5.—The theoretical total population of males and females of *L. coarctata* in the cage.

and between 26th June and 6th July were always more than twice as abundant as females. On 9th July, the sexes became equal in number, and subsequently the relative number of males to females gradually decreased until by the first week of August females were three times as abundant as males. This confirms the observations of previous authors. Gemmill (1927) stated that, on the average, males appear about a week earlier than females, and while this may not be entirely true, males are certainly at first by far the more abundant. Similar observations were also made by Gough (1946) and Long (1958) both in the field and in the laboratory. The early predominance of males was due to their more rapid build-up of population and their later scarcity due to their dying off sooner than the females.

It has been suggested (Gough, 1946), that the eggs require about a month for maturation. If the appearance of mature flies in the field follows a pattern roughly similar to that of emergence, but a month later, one would expect to find mature females first about the third week of July. They would not become numerous until the end of July and then the majority of the population would come to maturity during the next week or so. The appearance of eggs in the soil might be expected to follow a similar course. Taking mortality into account, one would expect that roughly between one-fifth and one-sixth of the females that emerged would come to maturity.

Absolute numbers of all stages.

The population estimates for all stages are shown in Table IV. Sampling for eggs was carried out on 12th March, the earliest date after the frosts on which

TABLE IV.

Populations of various stages of Wheat Bulb Fly.

Date	Sampling method	Stage	Mean population (1000's/acre)	Mean* standard error
12.iii.56	Soil cores	Eggs	1,556	± 199
12.iv.56	Plants	Larvae	227	± 45
31.v.56	Plants	Larvae	30	± 5
13.vi.56	Plants	Larvae	0	
	Soil cores	Pupae	377	± 106
21.vi.56–25.vii.56	Emergence cage	Adults	83	—
19.vii.56–22.viii.56	Estimated from recaptures inside cage	Mature females	7	
.ix.56	Soil cores inside cage ..	Eggs	226	± 95

* Analysis carried out on $\sqrt{n+\frac{1}{2}}$ transformation, hence standard error asymmetrical around arithmetic mean. Mean value given here.

it was possible to take discrete cores of soil. Twenty samples, each consisting of five cores of soil, 2½ inches in diameter and six inches deep, were taken at random and eggs were extracted by a flotation process similar to that of Salt & Hollick (1944). As many eggs had hatched, the population estimates were based partly on empty shells, hence they may be somewhat high, as well preserved shells

persisting from the previous year (also fallow) would be indistinguishable from those recently hatched.

Larval populations were estimated on 12th April, 31st May and 13th June by counting numbers in random samples of 100 plants and multiplying the mean number of larvae per plant by the mean number of plants per square foot. (The latter was estimated by taking plant counts from 20 one-foot-square random samples.)

On 12th April, 42 plants out of the hundred showed signs of infestation. There were 66 damaged tillers, but only 30 larvae, mostly in their second instar, were recovered. The estimate of larval population was lower than that subsequently found for pupae, but at this time secondary migration was in progess so the low estimate was possibly due to many larvae having temporarily left the plants. On 31st May, amongst 30 plants showing signs of infestation, 48 damaged tillers were found. Only four larvae were recovered, all in their second instar. The development of these seemed to have lagged considerably behind that of the majority of the population, as examination of the soil round the roots of the plants on the same day showed that almost all the larvae had by now pupated. On 13th June, eight plants showed a total of nine damaged tillers; no larvae were found. Soil samples were therefore taken and examined for pupae, the method of sampling and examining being similar to that used for eggs.

The adult population was estimated from the total number of flies emerging. It seemed possible that trampling might reduce the numbers emerging from the soil of the paths, so this was investigated by examining 10 soil samples (each consisting of five 2½-in. cores to depth of 6 in.) taken from the paths and an equal number from the untrampled soil amongst the wheat. If trampling had prevented flies from emerging, then it might have been expected that their remains would have been found in the soil from the paths. From each series of samples two dead pupae were recovered. This is roughly equivalent to about 330 in the whole of the cage. Originally there must have been a total of some 2,500 pupae of which about 550 emerged as flies. About 1,600 therefore still remained unaccounted for, and the soil sampling could not be regarded as providing any information on the effect of trampling on emergence.

The soil samples were also examined for eggs. None was found in those from amongst the wheat, but 20 were found in those from the paths. This is equivalent to 956 eggs in the whole of the cage and suggests a mean production of 33 eggs per mature female (*cf.* the estimate of Gough (1946) 30 to 50 eggs/female). However, about 36 per cent. of the females are believed to have been killed by marking, so this figure must be corrected to what it would have been if no deaths due to marking had occurred. This gives a new total of 1,500 eggs which is equivalent to 226,000 per acre or roughly 1/7th of the population of the previous year (see Table IV).

Observations on another part of Pennell's Piece (R. Bardner, private communication) suggested that egg populations there were roughly equal during the two years. This suggests that the reduction of population observed in the cage was probably due to the experiment. The mortality between pupation and emergence of flies was high (78%) and may have been partially due to trampling the soil of the paths. If no adults had emerged from the paths (which occupied ⅓rd of the area of the cage) then to compensate, the potential number of eggs should be increased by one-half and the reduction from 1955 to 1956 decreased from 1/7 to 2/9. Even so, about 70 per cent. of the pupae are still unaccounted for.

Factors which may have influenced the survival rate and fecundity of the adults are handling, disturbance and possible inadequacy of the food supply within the cage. These could not be investigated in the present experiment but will have to be taken into account in future work.

Discussion.

This is believed to be the first application of the marking and recapture technique to a closed insect community. With refinement and development the method may prove of value for the study of other insects as well as Wheat Bulb Fly. The method has three advantages:

(1) All the flies are of known age.

(2) Dispersal is prevented and a high proportion of marked flies is recaptured. Hence relatively low numbers are needed and labour requirements are low.

(3) Immigration of flies into the area is also prevented.

At present the technique is undeveloped but it can be improved. The high initial mortality attributed to marking should be reduced, and if possible insects should be labelled individually rather than according to date of emergence only. Handling may be harmful and should be minimised, therefore a balance between harming the flies through excessive handling and running the risk of having too little data must be found.

Although in the present study the mean rate of population decrease was found for the data as a whole, it would have been preferable to have treated each day's emergence separately. For this, however, much greater numbers of flies, say 30 to 50 a day, would have been needed.

More should be known of the effect of confining the flies. The area of the cage was large and a fair sample of the field was enclosed, but it is possible that not all the food substances available to the free-living fly were present. If so, this may have had an effect on the rate of maturation or on length of life.

Summary.

During the summer of 1956, a quantitative study of a field population of Wheat Bulb Fly, *Leptohylemyia coarctata* (Fall.), was carried out at Rothamsted.

The work consisted principally of a study of the development and decline of a population of adult flies. This was supplemented by observations on the populations of the immature stages.

Emergence was investigated by the use of a cage of fine terylene netting, 24 ft. long, 12 ft. wide, and 6 ft. high. This was erected in an infested wheat field shortly before flies were expected to appear, and was searched twice daily, at 10 a.m. and shortly before sunset.

A total of 293 male flies was caught during the 26 days from 24th June to 19th July. Of these, 186 appeared between 1st and 6th July. The highest day's catch was 40 flies on 6th July, by which date (inclusive) about 84 per cent. of the final total had emerged.

A total of 258 female flies was caught during the 35 days from 21st June to 25th July. Of these, about half emerged between 6th and 10th July. The highest day's catch was 37 flies on 8th, by which date (inclusive) 66 per cent. of the final total had emerged.

Population decrease was investigated by the method of marking and recapture. The newly emerged flies caught in the cage were marked with Artist's oil colours and released in the cage. The colour of the mark was changed daily so that the age of marked flies could be ascertained. A search was made for marked flies every three days and their numbers, marks and sex were recorded. From the recapture figures, estimates of the numbers of flies surviving at different times after marking were obtained. Mortality during the first day was very high, but after this numbers decreased at a steady rate. This initial high mortality was believed to be due to marking. The length of life of marked flies which survived this immediate effect was, however, not impaired, therefore the rate of population decrease was estimated from the recapture figures alone, that is, without reference to the numbers originally marked. The half-life of male and female populations was estimated as 7·3 and 11·1 days, respectively.

Application of the estimated rate of population decrease to the observed emergence figures enabled a general picture of the size and structure of the population to be obtained. The predominance of males over females during the early part of the season and the later predominance of females over males were explained.

Observations on the populations of the various stages showed that the mortality between pupation and maturation of adults was high, and that the egg populations inside the cage during the autumn of 1956 was only about 1/7th of that of the previous year. This reduction was not observed outside the cage and may have been due to the survival rate and fecundity of the flies being affected by the experiment. Further work will be necessary before this can be elucidated.

Acknowledgements.

It is a pleasure to record our gratitude to Dr. Marjory G. Morris and Dr. K. Mellanby for discussing and criticising the work at all stages. We are also grateful to Mr. D. Burton for making the field cage, to Messrs. F. Alston and M. Mann for assistance in the field, to Mr. V. Stansfield for photography and to Miss A. Simpson and Mr. B. Slater for assistance in preparing the figures.

Appendix.

Description of the Cage and Notes on the Climate within it.

The supporting framework consisted of jointed galvanised tubes and rods of the type used by horticulturalists for supporting fruit nets, etc. A rigid structure 24 ft. long, 12 ft. wide and 6 ft. high was constructed and covered with white terylene netting of mesh 18 holes per inch. Seams and corners were reinforced with strips of cotton binding which was treated with Granger's "Tropsol" solution to prevent rotting. The bottom of the cage was sealed by burying the foot of the net in the soil and an entrance was made by leaving an opening 44 inches long at one corner which could be closed by a zip fastener.

The cage remained in the field for three months, during which time much bad weather occurred. In spite of this, little damage was observed. During a period of gale-force winds the framework became bent, but this did not impair the efficiency of the cage. Small runs in the fabric were patched with pieces of netting stuck on with cellulose cement.

During the period 28th August to 1st September 1956, observations were made on temperature, relative humidity and windspeed both inside and outside the cage. Readings inside the cage were taken near the centre, those outside it, in the adjacent crop some 30 ft. from the cage. Temperature recordings were made on a Short and Mason continuous-recording thermograph, the thermometer bulbs being 4 ft. 2 in. above the ground, some 6–7 in. above the crop. Windspeeds inside and outside the cage were measured simultaneously by means of a pair of balanced Casella 3-cup anemometers. Three runs of two minutes each were made at each observation and their means compared. Anemometer readings were taken at two levels, namely 4 ft. 2 in. and 12 in. above ground. Relative humidity was determined by means of a Casella whirling hygrometer 5 ft. 6 in. and 12 in. above ground. Mean values of three readings were compared.

On cloudy or overcast days, temperatures inside and outside the cage differed little. On clear days, however, temperatures outside exceeded those inside by 2–3·5°C. at noon. At night no temperature differences were noted. In the mornings the rate of warming up within the cage was less than that outside, and in the evenings the rate of cooling was less.

In general, the relative humidity inside the cage was greater than that outside. At 5 ft. 6 in., the differences were slight, but at low windspeeds, when mixing of the air was poor, differences of 2–6 per cent. were observed.

Windspeed inside the cage was reduced, and within the range observed, was directly proportional to that outside (fig. 6). At 4 ft. 2 in. it was reduced by about one-half, and at 12 in. by about one-third.

The effect of the netting on light intensity was measured in the laboratory. There was a reduction of approximately 10 per cent. when the netting was new

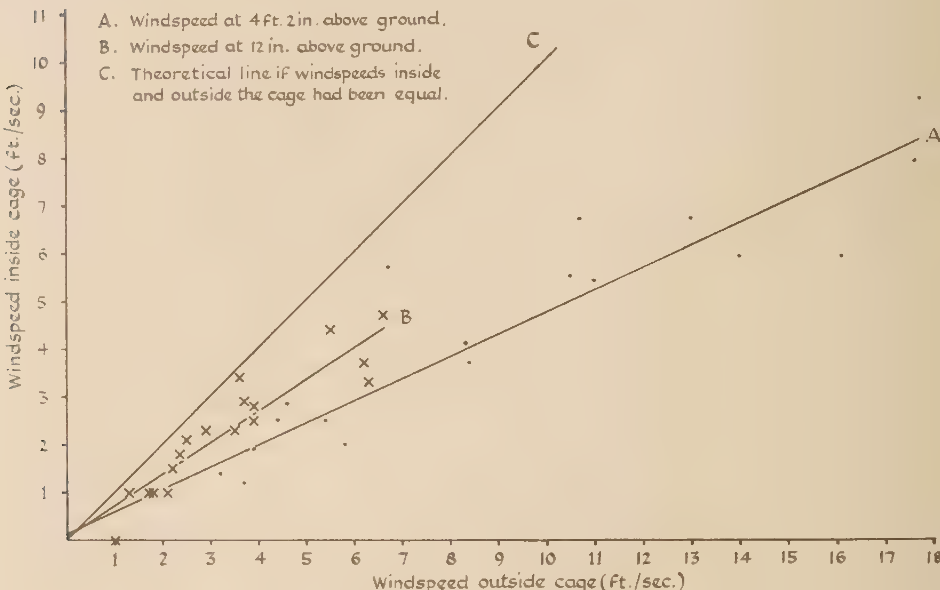

Fig. 6.—The relationship between windspeed inside and outside the cage.

and approximately 15 per cent. when it had become discoloured through standing in the field for three months.

Despite the differences between the climate of the cage and that of the field outside, there was no noticeable difference between the wheat inside and that outside.

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FIG. 1. General view of emergence cage.

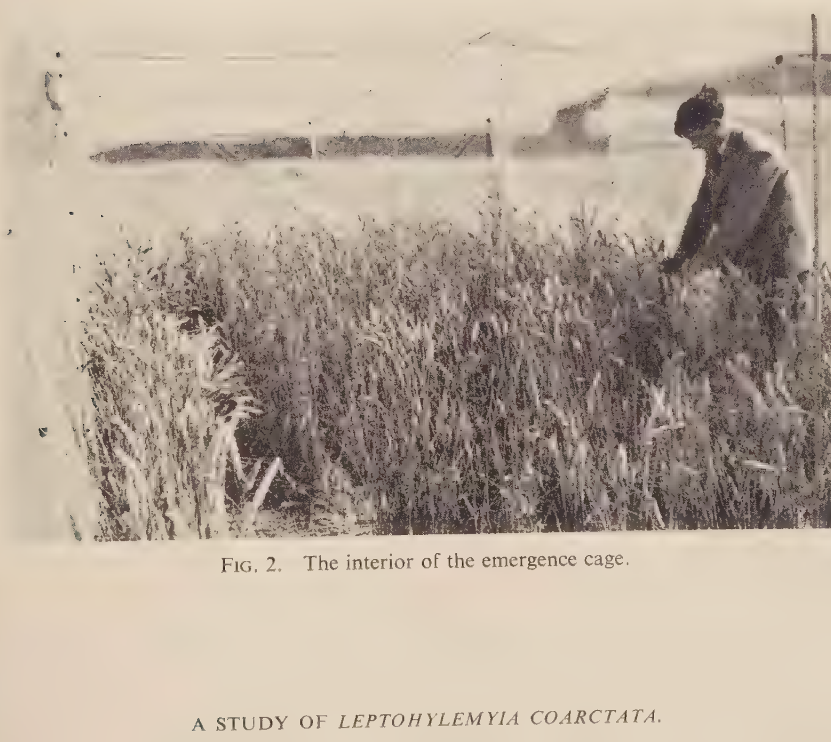

FIG. 2. The interior of the emergence cage.

OBSERVATIONS ON THE OCCURRENCE OF LARVAL INFESTATIONS OF WHEAT BULB FLY, *LEPTOHYLEMYIA COARCTATA* (FALL.).

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(Plate III.)

The influence of the previous crop on the level of larval infestation of winter wheat by the Wheat Bulb Fly, *Leptohylemyia coarctata* (Fall.), has attracted much interest for some years. Whilst it is generally well known that the heaviest infestations tend to occur after bare fallows, the area of such land is normally relatively small, and infestations follow a wide variety of crops which provide varying degrees of ground cover. Gough (1949) showed that much heavier populations followed fallow than a crop of any kind, but as his survey of 1945 covered a very wide area of Yorkshire, involving vastly different localities, different soil types and different proportions of the crops grown, it is not clear how far his results on interrelationships between larval infestation and previous crop may be applied to a uniform area. For purposes of comparison it may be considered that, in a uniform area, the major differences in the population levels reflect the influence of the previous crop on oviposition. Rothamsted Experimental Farm, which is on clay-loam and is on the western edge of the Wheat Bulb Fly area in southern England, grows winter wheat after a wide range of crops and presents suitable conditions for the study of their effects.

Effect of the Previous Crop and Manurial Treatment on Oviposition.

In a survey of larval infestation in 1954, samples were taken from wheat following 10 different crops grown the previous year, whilst in 1955 and 1956, samples were mostly taken from wheat following fallow. Each plot to be sampled was divided across its length into five sub-plots. Two individual samples were then taken from each sub-plot at points fixed by random numbers as to the row of plants and the distance along it, the edge rows being excluded. The individual samples consisted of one foot-row of wheat taken by removing to the laboratory all the plants falling within a six-inch gauge placed along two adjacent rows. The results of individual samples were bulked to obtain the plot sample of ten foot-rows from which were made the larval population estimates given in Table I. The general location of the Rothamsted plots is shown in a plan in a preceding paper (Long, 1958, p. 77).

In considering the results careful note must be taken of the ploughing date, as the early ploughing of clover and ryegrass rendered these plots effective fallows throughout the egg-laying period of mid-July to early September. It can then be readily seen that the highest population of larvae followed fallows. The next highest populations followed potatoes, a low open cover crop, being at Rothamsted of the order of between one-fifth and one-tenth of that following an equivalent fallow. Much lower populations followed the tall crops of beans and wheat whilst the lowest estimates followed the mat covers of grass, leys and lucerne. These results are in general agreement with those of Gough (1949) in terms of the relative order of the mean populations he obtained for Yorkshire for fallow, potatoes, cereals and beans.

TABLE I.

Estimates of larval population in wheat following various crops.

Previous crops	Situation	Ploughing date	Number of plots sampled	Number of larvae/acre (in thousands)		
				1954	1955	1956
Barley	Fosters	12.x.53	4	167	—	—
Beans	Hoosfield [1] : 4-course experiment ..	—	2	—	—	15
Clover	Long Hoos IV: 6-course experiment	10.vii.53[2]	5	1078	155	802
	Stackyard [3] : 6-course experiment ..	3.vii.53[4]	5	502	—	—
Cut grass	Fosters	12.x.53	4	5	—	—
Fallow	Broadbalk	10.vi.53[5]	7	1477	277	635
	Long Hoos VII	—	4	—	40	22
	Wheat & Fallow	3.ix.53[6]	2	1038	367	583
Ley	Long Hoos I & II : Deep cultivation	30.ix.53	4	35	—	—
Ley: grazed	Fosters	12.x.53	4	7	—	—
Lucerne	Fosters	12.x.53	4	4	—	—
Potatoes	Long Hoos I, II & III : Eyespot expt.	6.x.53	8	170	—	127
	Roadpiece [3]	21.x.53	10	12	—	—
	Little Knott	—	1	—	—	44
Ryegrass	Hoosfield : 4-course experiment ..	9.vii.53	4	2023	359	—
Wheat	Broadbalk	—	4	—	—	11
	Geesecroft	23.ix.53	1	7	—	—
	Long Hoos VII	—	4	—	—	1

[1] Shown on plan (Long, 1958, p. 77) as Four-Course.
[2] Reploughed 17.ix.53.
[3] Situated at Woburn Experimental Station, Bedfordshire.
[4] Reploughed 16.ix.53.
[5] Spring-tine harrowed 29.vi.53, 7.vii.53; thistlebar 11.ix.53.
[6] Spring-tine harrowed 9.vi.53, 1.vii.53, 17.vii.53.

When the figures are examined in detail in relation to manurial treatment (Table II), it appears that dung may influence the infestation. In 1954, plot 2 had, with the exception of plot 12, significantly more larvae than any other of the Broadbalk plots sampled, thus confirming the observations of Raw (1954), and on Hoosfield (the 4-course experiment), similar results were obtained as compared with the straw (*i.e.*, non-dung) plots ($P<0{\cdot}001$), whilst some of the effect of the dung on the larval population was found to persist in the fifth year after application ($P<0{\cdot}05$). Part of the effect of the dung appeared to be attributable to the straw component which disappeared with time ($P<0{\cdot}05$). On Broadbalk, in 1955, the population following dung ranked amongst the lower values observed but in 1956 it was once again the highest, being significantly so except for plots 12 and 13. The position with these latter two plots in 1954 is curious, with plot 12 having more than twice the population of plot 13. The difference between these plots appeared again in 1955 but was not significant and was absent in 1956. Rape cake on plot 19 in 1955 was clearly the lowest, but in 1956 the population was nearly eight times greater and was of a similar order to

the other plots. The effects of the other manurial treatments were not wholly consistent and generally relatively small whilst the results obtained on Long Hoos IV in 1954 could follow from the effect of adjacent crops as given later in this paper (p. 119).

TABLE II.

Estimates of larval populations in wheat following effective fallow.

	Manurial treatment	Number of larvae/acre (in thousands)		
		1954	1955	1956
Broadbalk[1]	Plot 2 : dung	1931	131	951
	3 : no manure	1292	102	—
	10 : N	1307	348	450
	11 : N P	1321	407	—
	12 : N P Na	1742	501	646
	13 : N P K	857	378	675
	14 : N P Mg	—	370	574
	16 : N P K Na Mg	—	363	515
	19 : rape cake	—	80	624
Hoosfield [2] (4-course experiment)	1st year after dung	2773		
	5th year after dung	2084		
	1st year after straw	1851	359[3]	—
	5th year after straw	745		
Long Hoos IV [4] (6-course experiment)	1. P K	915		
	2. N K	1321		
	3. N P	849	155[3]	—
	4. N P K	1227		
Wheat & Fallow	Exhaustion	1038	367	583

[1] Broadbalk manurial treatments (per acre):—
Dung — 14 tons.
N — 4 cwt. sulphate of ammonia.
P — 3½ cwt. superphosphate.
Na — 1 cwt. sulphate of soda.
K — 2 cwt. sulphate of potash.
Mg — 2½ cwt. sulphate of magnesia.

[2] Hoosfield (4-course experiment) manurial treatments (per acre):—
Dung — 12½ tons: Straw — 7½ tons.

[3] Mixed plots at random.

[4] Long Hoos IV treatments (per acre):—
N — 1½ cwt. sulphate of ammonia: P — 1½ cwt. superphosphate: K — 1 cwt. muriate of potash.

From the general observation that the highest infestations follow a bare fallow it has generally been assumed that the Wheat Bulb Fly will lay at random in any available fallow. Reference to the fallow and wheat plots in Table I for Long Hoos VII in 1955 and 1956 shows that the population was well below that of the other fallows, being, in 1956, less than one-tenth of the Broadbalk estimates. The site of Long Hoos VII had previously been under sugar beet and, as can be seen in fig. 1 of a preceding paper (Long, 1958, p. 77), is relatively close to the infestation centres of the 6-course experiments and the Wheat & Fallow strips, and flies were known to be present. The results show, therefore, that flies do not necessarily lay in any available fallow, but may be influenced by some other factors as yet unknown. It must be remembered, in interpreting these results on fallows, that different sections of the fields are involved each year and obviously much more work must be carried out if, for example, the effects of the manurial treatments are to be completely assessed.

Effect of Crop Density on Oviposition.

It has been known for some years, as previously stated, that egg-laying occurs freely in bare fallows, whereas, in wheat, relatively little takes place (Table I). Observations in the past, of infestations following various crops, showed that those following low crops such as sugar beet, potatoes, and dwarf field (canning) peas were likely to be heavier than those following taller, denser crops such as wheat, field beans, etc. This suggested that a vertical stand of wheat might represent a flight barrier which would interfere with the subsequent egg-laying behaviour. However, areas of wheat may be thinned to produce sparse patches in the subsequent crop. In order to investigate the relative effects of fallow and thin patches of wheat on egg-laying, an experiment was set up on Long Hoos VII (Long, 1958, p. 77, fig. 1) in the spring of 1954, consisting of four sets of repli-

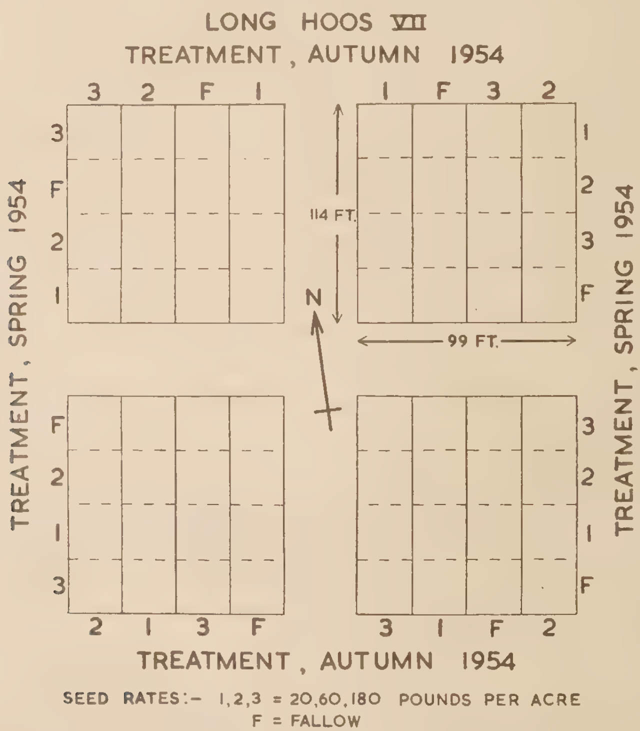

Fig. 1.—Plan of an experiment on Long Hoos VII to show the effect of the plant density on oviposition.

cates of randomised plots incorporating a fallow and spring wheat sown at three different densities in which the replicates were surrounded and individually separated by headlands sown at the highest density of 180 lb./acre. In the first year the aim was to provide conditions of stands of wheat at different densities, together with a fallow, during the laying period in the summer of 1954 (Pl. III). For this purpose Koga II spring wheat was used. In the autumn of 1954, the experimental design was rearranged so that the strips of wheat were sown across the sites of the strips of the previous spring (fig. 1). In the autumn of 1955 the entire experimental area was sown at the uniform rate of 165 lb./acre. In both these latter sowings the winter wheat, Cappelle, was used. Stem counts just

before harvesting in 1954, and again in 1955, showed that the seed rate ratio was not maintained till the harvest, the thinner wheat tillering more freely than the denser. However, differences in the density of the stands did persist, at a less marked level, as can be seen from the rougher appearance of the surface of the low-density plots in Plate III.

As with the other areas of winter wheat, the very wet autumn of 1954 delayed sowing to such an extent that by the time of sampling in the spring of 1955 the young wheat was still in the single-shoot stage with the outer leaves still uncurled, and not surprisingly, therefore, very few larvae were found in samples taken from sub-plots (four per plot) following any of the various conditions of the previous summer, and the results were inconclusive.

The summer and early autumn of 1955, however, were dry and warm and presented satisfactory conditions for oviposition, and the experiment was extensively sampled in the spring of 1956. Five samples, consisting each of one foot-row of plants, as earlier described, were taken from each sub-plot, making a total of 80 samples for each treatment and 320 samples in all.

TABLE III.

The effect of the density of stands of wheat during the oviposition period on the subsequent estimates of larval populations.

Summer 1955	Spring 1956			
Wheat density (seed rate per acre)	In wheat uniformly sown at 165 lb./acre			
	Plants/acre (1000's)	Stems/acre (1000's)	Larvae in 80 foot-row samples	Estimated larvae/acre
180 lb.	1022	2725	1	900
60 lb.	1051	2848	3	2700
20 lb.	1044	2872	3	2700
Bare fallow	1139	3773	24	21800

For details see text.

From the results given in Table III it can be seen that the wheat following fallow carried more than 20 times the population found in the wheat following the "normal" density of wheat sowing. Remarkably few larvae were found in the wheat following the other treatments; in the 3,433 plants, comprising 9,300 stems, examined from these treatments, only 7 larvae were found. Thus, in spite of the considerable amount of material examined in these samples, no conclusions could be reached as to the effects of the treatments.

Effect of a Vertical Obstruction.

A study of the effect of a vertical obstruction such as a stand of wheat was made by sampling for larvae in the spring of 1955 and 1956 on the Wheat & Fallow plot. The plan of the experiment is given in fig. 2. The plot is divided along its length and the two halves (designated A and B) are cropped alternately, the uncropped half remaining fallow. The sector under wheat is further subdivided into four, three of which are cropped, whilst the fourth also remains fallow. As a result of this procedure, when egg-laying occurred in the fallow half (B) in 1954, part of that fallow (sub-plot B3) was bounded on the southern

edge by the wheat (3 ft. 6 in. high), whilst the adjacent sub-plot (B4) was not so bounded being opposite the fallow (sub-plot A4) in the wheat sector.

In the spring of 1955, sets of five pairs of six-inch samples were taken at random from each alternate row of sub-plots B3 and B4, beginning at the southern edge, the edge row itself being ignored. As with other winter wheat,

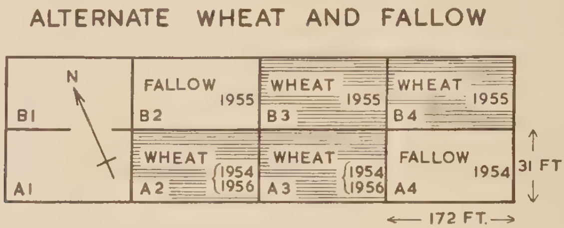

Fig. 2.—Plan of the treatments in the alternate Wheat & Fallow experiment. (Sub-plot B1 was wheat in 1955; and A1, wheat 1954 but fallow in 1956.)

the cultivation of the Wheat & Fallow plot in the previous autumn had been delayed and sowing did not take place until December. It was found on examining the samples that many plants had been superficially damaged, the larval entrance tunnel having been apparently discontinued. There were three times as many damaged plants as there were plants containing larvae, and this, when contrasted with the normal excess of less than 1·5 times that of the infested plants, suggests that some repellent factor such as the BHC residues from the seed dressing was still effective in the hatching period.

From the results (fig. 3) it can be seen that in that part of the experimental sub-plot B3 which had been adjacent to the previous stand of wheat in sub-plot A3 very few larvae were found, but the number increased as the distance from

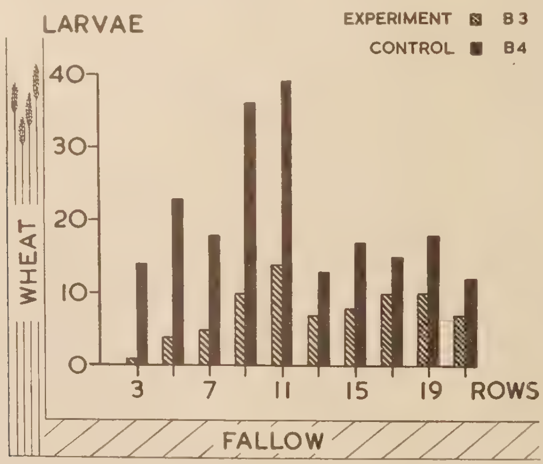

Fig. 3.—Larvae occurring in alternate rows of wheat following a fallow adjacent to a crop of wheat.

this stand of wheat became greater. It can also be seen from the control sub-plot B4 that whilst other fluctuations were occurring the numbers of larvae of B3 never rose to the same level.

If the results be expressed as the ratio of larvae per row of the two sub-plots,

the shadow effect of the previous stand of wheat on sub-plot A3 becomes apparent (fig. 4). From these results it can be seen that a marked effect extended some 13–15 rows into the crop; that is, a vertical stand 3 ft. 6 in. high produced an effect over a horizontal distance at least twice as great. The residual difference between the mean populations occurring in the centres of the two plots may be attributed to factors other than that under immediate consideration.

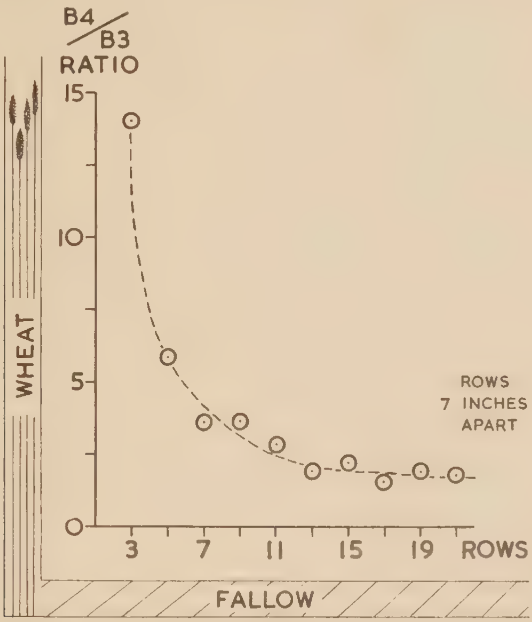

Fig. 4.—The shadow effect of the crop of wheat in fig. 3 on oviposition. (For details see text.)

When the experiment was repeated by sampling for larvae in the spring of 1956 the sub-plots involved were A2 (fig. 2) which, while fallow, had been opposite a fallow (B2) the previous summer and A3 which, while fallow, had been adjacent to the wheat on B3. From this it can be seen that the geographical orientation had been reversed. The results obtained confirmed those of the previous year except that the area affected was not so great, extending up to 4 ft. 6 in. from the base of the crop.

The shadow effect referred to above could have been responsible for the effects of dung on oviposition observed earlier in the 4-course experiment (p. 115) as the contrasting straw plots were adjacent to a tall standing crop.

Discussion.

The field observations show that the effects of the previous crop fall into a distinct order. The heaviest infestations follow the bare fallows, the next heaviest follow spaced dwarf crops, such as potatoes, which provide varying degrees of ground cover of the open foliage type. Much smaller infestations follow tall crops such as wheat and beans whilst the smallest infestations followed the grass mats.

The question now arises as to how far these conclusions on the relative effects of the previous crop can be applied to areas other than Rothamsted, although in general the observations confirm the findings of Gough (1949) in his survey of Yorkshire.

The situation at Woburn is of particular interest. The soil is light and sandy and wheat is not apparently grown to any great extent in the region. The six-course experiment on which clover plots given in Table I were situated was relatively close to an area of permanent wheat, and the population for these plots was about one half of that for the equivalent plots on the Rothamsted clay-loam. It had been observed at Rothamsted that the population in wheat following potatoes was about one-sixth of that found in wheat following early-ploughed clover (see p. 114). At Woburn, however, the population following potatoes was less than one-fortieth that following early-ploughed clover. The explanation of this difference would appear to lie in the matter of distance between the potatoes and the sources of infestation; at Rothamsted this was only 100 yards, whereas at Woburn the two fields were a mile apart, although it is not known if additional centres of infestation nearer the potato field had existed on property outside the experimental farm. Distance, too, could explain similar differences in population incidences following wheat at Rothamsted; on Broadbalk this was about one-thirtieth of that for the adjacent Broadbalk wheat following fallows, whereas on Geesecroft, half a mile away, it was about one-twohundredth of this fallow figure. Gough (1949) notes the absence of larvae of Wheat Bulb Fly in three fields of wheat after fallow which were about one mile from other fields known to be infested. As a period of two to three weeks exists between the emergence in the infestation centres and the subsequent oviposition, these observations would support an impression given earlier (Long, 1958) that in the border areas of Wheat Bulb Fly infestation, where wheat fields are well separated, the flies do not normally move far from the infestation centres but tend to exist as a series of localised populations centred about the emergence fields. From this it may be concluded that the effect of the previous crop will be modified by the distance from the nearest infestation centres, a conclusion also reached by Rostrup (1924) in respect of the infestation of fallows.

The differences between the infestations following the crop groupings of fallow, dwarf open crops, tall crops and grass mats were appreciable and it seems reasonable to infer that they mainly reflect the effect of those crops on oviposition. Thus, it is of fundamental interest that this pest of cereals should, paradoxically, fail to lay to any extent in wheat, whilst laying most freely in bare fallows. This question has been raised repeatedly by those coming into contact with the fly.

The female fly has often been observed, after alighting on a head of wheat or the uppermost leaf, to run down the stem, but after a distance of some 18 inches to turn round, come up again and eventually fly off. The course of such movements was frequently very erratic, with the fly stopping for periods, but the movements did not appear to involve feeding, and would be consistent with the observation of Long (1958) from the results of sweeping that the females went deeper into the crop than the males. If the gravid fly is normally dependent on contact with the soil to evoke the laying stimulus, as appears to be the case, this pattern of behaviour would materially reduce the number of occasions when that eventuality was likely to occur in wheat. On the other hand, with flies alighting on dwarf crops the same pattern of behaviour would bring the fly into contact with the soil, and flies pitching on the leaves of sugar beet have been observed to reach the soil in this way.

As contact with the soil is important for oviposition, it may be inferred, from the failure of the fly to infest the grass mats, that an effective barrier can be provided in the form of a dwarf dense ground cover. Wheat following mustard grown for this purpose at Rothamsted has been found to be apparently free of infestation.

The effects of the previous crop, as observed in the field, may possibly, therefore, be explained by the fact that, if egg-laying takes place as a result of

contact with the soil, the opportunity for this event to occur depends on the plant density of the crop cover and its height in relation to the distance the fly will normally descend in the crop. The oviposition behaviour of the fly is therefore linked, to the advantage of the species, with the agricultural practice of sowing winter wheat after fallow and open dwarf crops.

The life-cycle of the fly also coincides very well with the development of the food-plant. The fly is known to lay its eggs in late summer, and, after a period of development, the embryos remain in a state of diapause until early the next spring. During the same period an annual cereal such as wheat has fruited and died and the new crop sown in the autumn has grown into young plants. The other known food-plants, which consist of some of the coarser perennial grasses (Gemmill, 1927; Gough, 1946; Stokes, 1955), also die back in the winter. The larvae hatch just as the plants are approaching the period of maximum tillering, which affords a continuous supply of food in the right stage of development. The fly lacks an adequate mechanism for laying eggs in plant tissues and, since both the eggs and larvae are easily desiccated, eggs laid in the soil both experience some certain measure of protection from this hazard and are also in a favourable position to infest the developing shoots of the new crop.

When considering the effects of the manurial treatments on the fallows it was shown that dung appeared to produce an effect both in 1954 and 1956 but not in 1955. This effect has also been observed by Raw for 1954 but not for 1955 (Raw, 1954, 1955). In an experiment on Pennell's Piece, which is adjacent to Broadbalk, Raw (1955) took samples for eggs on 23rd September 1954. Subsequently these plots were examined for larvae on 7th April 1955 and showed for the intervening period for both the control and the dung-treated plots a survival of 10 per cent. This would support the contention of Raw (1954) that the soil conditions would be more likely to affect oviposition than the survival of the eggs and would suggest that the relatively larger populations on the dung plots were due to increased laying. In view of this the absence of this effect in 1955 is interesting. The summer of 1954 when egg-laying took place was cold and wet whilst the summers of 1953 and 1955 were dry. Should the effect be due to organic residues in the soil (Raw, 1954) its absence in a wet year suggests a possible loss by leaching or the relative absence of specifically conducive conditions when the soil in all the plots was wet. It must be remembered that the effect of dung in dry years may be associated with other factors such as the nature of the soil structure and the extent of cultivation as stated by Rostrup (1924) and confirmed by Raw (1955).

The distribution of the few larvae which infested the wheat (after wheat) on Long Hoos VII suggested that flies penetrating the crop and reaching the soil laid very few or only one egg on each occasion, which would agree with the results obtained by Gough (1946) from egg counts. An analysis of the distribution of larvae in wheat following the fallows showed that the behaviour in oviposition was similar both in the number of eggs laid on each occasion and in being at random. A plant and tiller count in this experiment showed that in a wheat plot, after a fallow, which had 1,139 thousand plants and 3,773 thousand tillers per acre there were 100 thousand more plants and 950 thousand more tillers than in corresponding plots following wheat. This substantial increase in both plants and tillers would be to the advantage of a heavy infestation in wheat following a fallow.

The maximum effect of a stand of wheat on egg-laying in an adjacent fallow was obtained when the stand was on the south-west border and therefore could present the greatest contrasts of light and shade. When the situation of the two sites was reversed and this contrast was almost absent, the effect on the egg-laying remained but was much reduced in its extent. From this it appears that such stands of wheat may affect egg-laying by producing optical effects which influence the flight path. This would accord with a quotation by Rostrup (1924)

of observations by Hedlund in which flies were seen gliding down over the soil in a fallow field in which eggs were subsequently found.

Summary.

The effect of the previous crop on the subsequent infestation of winter wheat by the Wheat Bulb Fly, *Leptohylemyia coarctata* (Fall.), mainly on the clay-loam of Rothamsted Experimental Farm has been investigated for the years 1954 to 1956. By far the highest larval populations followed fallows, the next highest potatoes, which are a low, open cover crop, whilst much lower populations followed the tall crops of beans and wheat, and very small infestations followed the grass mat covers. This confirms the results of previous workers under different agricultural conditions.

Previous applications of dung and straw influenced the infestation following fallow in dry summers but not in a wet year. The effects of other manurial treatments were inconclusive.

An experiment designed to determine the effect of the crop density on oviposition was inconclusive due to the failure to establish an infestation.

Wheat was shown to influence the flight path and to interfere with local egg-laying behaviour, producing a horizontal effect of up to twice its own height.

Apart from the foregoing factors, at Rothamsted, where the wheat fields are well separated, the differences in the level of infestation that were observed could be explained by close proximity or otherwise to a centre of heavy fly infestation.

Reasons are put forward for suggesting that the effect of the previous crop on oviposition may be interpreted in terms of the opportunity existing for contact with the soil rather than as a preference on the part of the fly.

Acknowledgements.

I wish to express my appreciation to Mrs. B. Copleston and Miss J. Balshaw for their assistance with the examination of field material and to Mr. D. H. Rees for help and advice in the statistical analysis of the nature of the distribution of larvae in the field. I would also like to thank Dr. K. Mellanby for reading this manuscript.

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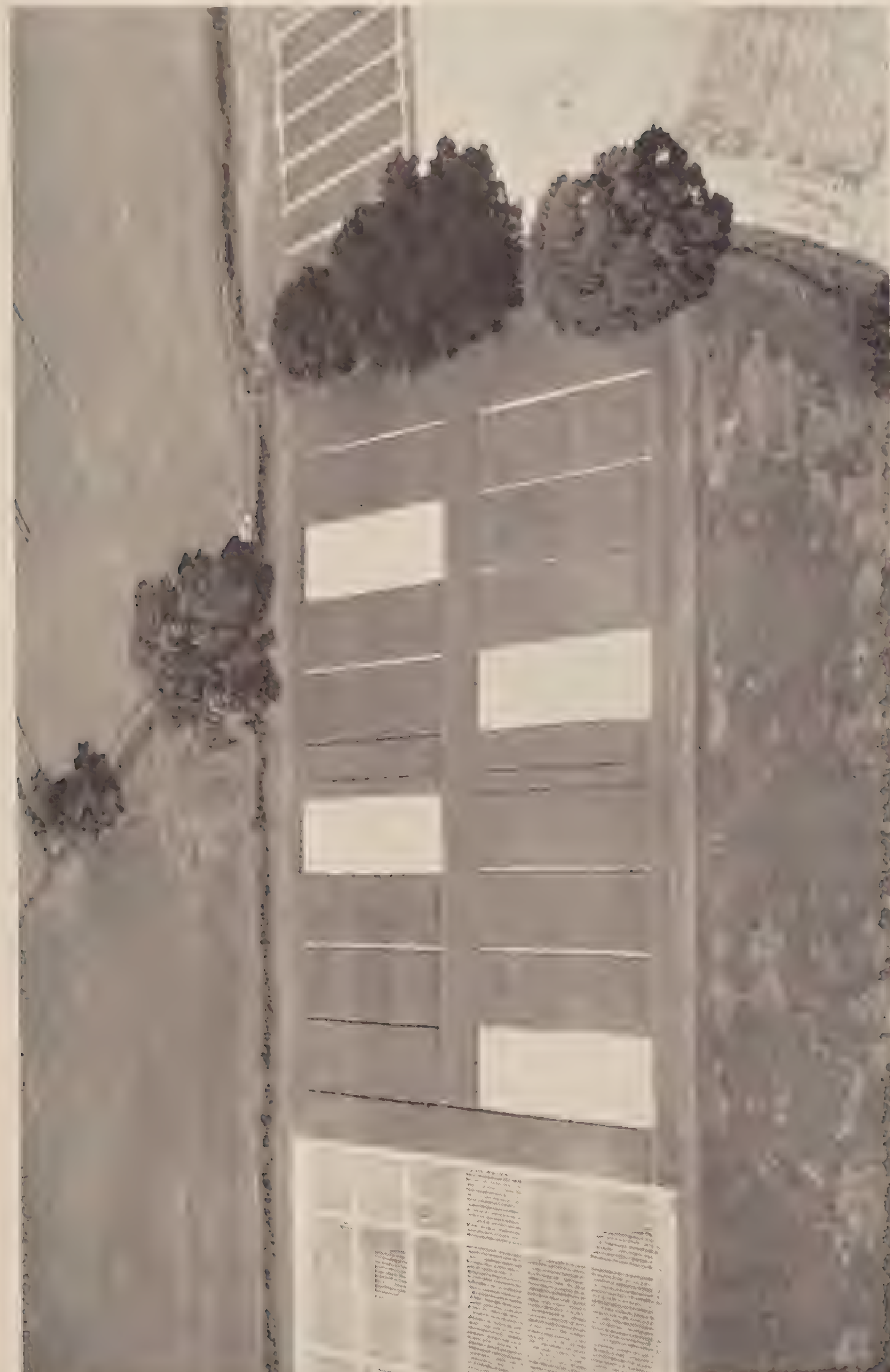

The appearance of the wheat in the experiment on Long Hoos VII involving different plant densities. (Reproduced by kind permission of Aerofilms Ltd.)

THE ERADICATION OF *GLOSSINA MORSITANS SUBMORSITANS* NEWST. IN PART OF A RIVER FLOOD PLAIN IN NORTHERN NIGERIA BY CHEMICAL MEANS.

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Glossina morsitans Westw.* infests one-sixth of the area of Northern Nigeria. The fly is of great economic significance to a valuable, entirely native-owned, stock-raising industry. Recently it has become apparent that there are considerable differences in the ecology of this fly in the Guinea and Sudan savannah zones,

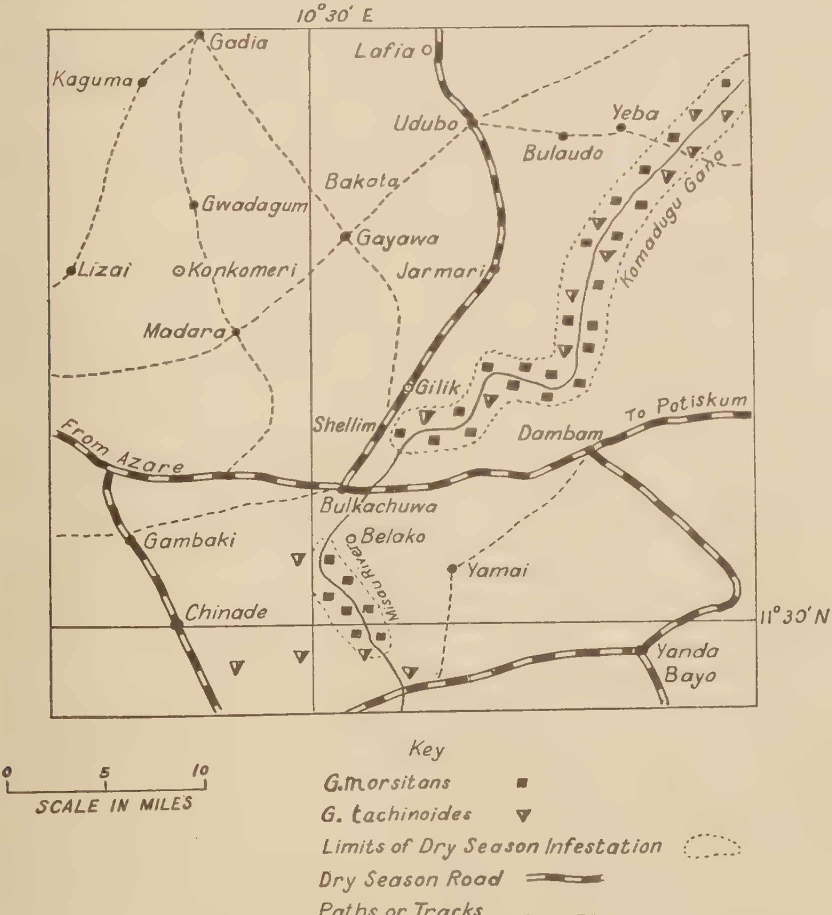

Fig. 1.—*Glossina* distribution, Misau river, Northern Nigeria.

* Throughout this paper the subspecies *submorsitans* Newst. is implied when reference is made to *G. morsitans*.

respectively. In the former, its distribution is relatively widespread and diffuse whereas in the latter it is restricted to linear strips associated with river flood plains. The area we are concerned with lies in the Sudan savannah zone (Keay, 1949) in an important cattle-raising area. Much of the fertile river plains is rendered unusable to livestock because it is infested with tsetse, cattle being forced to exist in the dry season on sparse vegetation on the upland, watering from wells that may be 90 feet deep, or else to migrate southwards to the moister areas of the Guinea savannah zone, frequently passing through other belts of *G. morsitans*. The fact that, in this part of the Sudan zone, the distribution of *G. morsitans* is in linear strips associated with river flood plains suggested that control measures might be effective. The area to be described is on the Misau river and is 30 miles from the Gadau tsetse research station, which functioned in the early 1930's. It is located approximately at north latitude 11°30′ and east longitude 10°30′ at an altitude of about 1,300 ft. The infestation which is the subject of the present paper is the southern extremity of the linear belt of *G. morsitans* that follows the flood plain of the Misau river, which later becomes the Komadugu Gana and flows to Lake Chad; it covers an area of some seven square miles and is separated from the main focus by a natural barrier, five miles wide, at the crossing of the motor road from Azare to Potiskum (see fig. 1). The area is also infested with *G. tachinoides* Westw. Eradication measures against *G. morsitans* were undertaken in this 7-sq.-mile area and were completed in the first four months of 1956. Although measures were also taken to control *G. tachinoides*, these are only referred to when they have a bearing on the subject of the paper.

Climate and Vegetation.

The climate at Gadau has been described in detail by Buxton & Lewis (1934) and by Nash (1937). It is essentially similar in the area described here. There is a severe dry season lasting from October to May. Rain is brought by the south-west monsoon but most of it falls in a series of severe thunderstorms accompanied by high wind from the north-east. The rainfall averages 30 in. annually. The maximum temperature is recorded as 109°F. and the mean maximum as 91·6°F. The absolute minimum is recorded as 46°F. and the mean minimum as 66·6°F. for a similar part of Northern Nigeria. On the upland the relative humidity varies from 90 per cent. at dawn and 60 per cent. in the afternoon during rains, to 35 per cent. at dawn and 7 per cent. in the afternoon at the height of the dry season. Thus the dry-season conditions for tsetse are severe.

The vegetation of the area falls clearly into the Sudan zone (Keay, 1949). The area differs from that described by the writers mentioned above in that there is no meadow pan. There are four major constituents, the relations of which are indicated in fig. 2.

(a) The upland savannah woodland, in which the commonest tree species are *Combretum glutinosum*, *Terminalia avicennioides*, *Strychnos spinosa*, *Amblygonocarpus Schweinfurthii*, *Prosopis africana*, *Piliostigma reticulatum*, *Bombax buonozense*, *Gardenia* spp., *Annona senegalensis*, *Anogeissus leiocarpa*, *Dalbergia hostilis*, *Guiera senegalensis*, *Commiphora africana*, with scattered examples of *Tamarindus indica*, *Ficus* and *Acacia* species. Much of the upland is however under cultivation.

(b) The river flood plain, which differs from the upland in that there are open glades and seasonal swamps. There is very little cultivation. The woodland is usually not so thick and the grass is taller. The commonest tree species here are *Combretum lecananthum* (?), *Annona senegalensis*, *Piliostigma reticulatum*, *Ximenia americana*, *Khaya senegalensis*, *Pseudocedrela Kotschyi*, *Stereospermum Kunthianum*, *Gardenia* spp., *Mitragyna inermis*, *Sterculia setigera*, *Daniellia Oliveri*, *Balanites aegyptiaca*, *Strychnos spinosa*, *Ziziphus mucronata*, with

scattered examples of *Ficus* and *Acacia* species and thickets, based on termitaria, comprising *Tamarindus indica*.

(c) Forest islands scattered through the flood plain, often on slightly higher ground and usually, but by no means always, associated with watercourses, either the one in current use by the river, or with the many subsidiary courses.

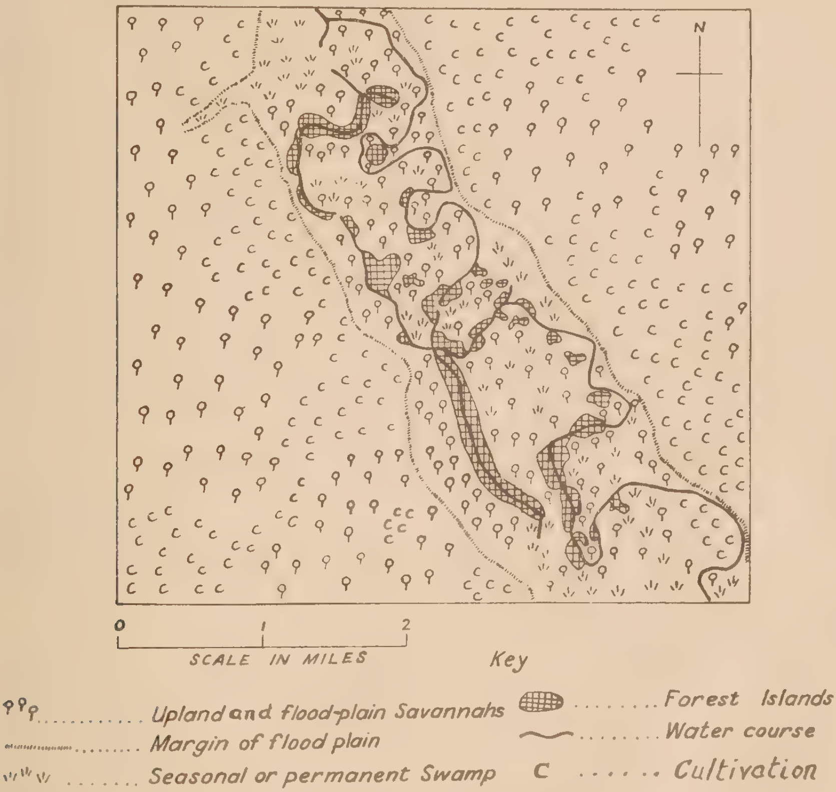

Fig. 2.—Misau river. Vegetation map.

The upper canopy is evergreen and is formed of the crowns of trees such as *Celtis integrifolia*, *Diospyros mespiliformis* and *Tamarindus indica* supporting a tangled mass of creepers such as *Capparis corymbosa* and *Acacia ataxacantha*. There is a thick under-storey of shrubs such as *Ziziphus mucronata* with other unidentified species and numerous *Diospyros* seedlings.

(d) Along the watercourses the commonest woody species are *Salix Ledermannii*, *Syzygium guineense*, *Mimosa pigra* and *Mitragyna inermis*.

The Distribution of *G. morsitans* in Relation to Vegetation and Food Supply.

The general outline of the focus enclosed an area of seven square miles. Most of the upland was under cultivation to the margin of the flood plain; in other areas, where the upland savannah woodland approached the flood plain, there was dispersal of *G. morsitans* into the woodland during the rains. Due to the degree of cultivation such dispersal was very slight in this area. The upland was completely evacuated by *G. morsitans* during the dry season. At the height of the

dry season most of the population of *G. morsitans* spent most of the day in the evergreen forest islands, and swarms of the flies were to be found here at this time of the year whilst, in the more open country between the forest islands, flies could only be found in low density. This relationship has been described in detail by Nash (1937). The main difference, as already stated, was that there was no meadow pan in this area.

In May 1955, it was found that *G. morsitans* was active from 7.00 a.m. to 8.30 a.m. at the edges of the forest islands. As the temperature rose the tsetse retreated into the islands, together with the wart-hogs which were the main source of food. A food supply was thus constantly available under the most favourable conditions. During the day many tsetse rested on tree trunks up to about 7 ft. from the ground. The proportion of females in the catch outside the islands was 1 per cent. but inside it rose to 35 per cent. More females were obtained if flies were caught off tree trunks and most of the males were intermediate or replete. Viable puparia were found in dry wallows made by wart-hogs in the forest islands as here the soil was soft and friable and not so dry and hard as elsewhere. Apart from the dry-season concentration in the forest islands, a few individuals of *G. morsitans* could be found in areas of scattered *Mitragyna inermis* until fairly late in the dry season. The leaves of this tree are very late to fall, which no doubt accounts for this. Occasional individuals of *G. morsitans* could be found associated with isolated tamarind trees (*Tamarindus indica*). As the rains broke, it was found that the density in the forest islands fell, more tsetse could be caught in the woodland and open areas and the population became more hungry, probably because of the dispersal of the food supply.

Wart-hogs were numerous in the area. The local inhabitants had killed off most of the game, but being Mohammedans did not hunt wart-hog, which, apart from occasional herds of cattle, must have been the main source of food for the flies. Duiker, oribi and gazelle were present but not numerous. The occasional kob was seen. Two buffalo were in the area for a short period only.

Possible Methods for Eradication.

An attack on the vegetation of the evergreen forest islands was considered but it was soon realised that both the wart-hog and the tsetse would disperse, make use of lesser thickets and lead to the situation which has developed before with such means of control, namely a much greater clearing programme than that originally deemed necessary. It was estimated that clearing would have cost at least £6,000.

Aerial spraying was not adopted because of the expense, because meteorological conditions were not likely to be favourable and because it was unlikely that the spray would penetrate the canopy of the evergreen forest islands.

It would have been difficult to organise a good game-destruction technique and cattle could not be excluded from the area. The animal health aspect demanded a prompt solution, £40,000 worth of cattle having died or been slaughtered the previous year as a result of trypanosomiasis.

It soon became evident that the tsetse population should be dealt with where it was most concentrated and that the best way of doing this would be to put a residual insecticide in the forest islands. It was expected that, with the absence of rain, the degree of shade in the forest islands and the lack of new growth of leaves and grass, the insecticide would show good persistence. The method would be relatively inexpensive. In fact, the cost of the insecticide and the labour to apply it amounted to £700.

Little advice was available locally with regard to insecticides on vegetation under conditions prevailing in Northern Nigeria. It was decided to follow, where applicable, the technique used in Kenya for the control of *G. palpalis fuscipes* Newst. (Wilson, 1953). DDT wettable powder was chosen because it was

comparatively less toxic to man than some other insecticides and could be handled safely by local illiterate labour. It had been reported as giving a more persistent deposit on vegetation than emulsions or oil-borne sprays and was clearly visible after application on vegetation. It was easily transported and mixed with water from the river. Four Oaks Kent knapsack sprayers were used for the application.

The Application of DDT.

Preliminary trial.

In the early rains of 1955, an experimental spraying was carried out in one of the forest islands. DDT wettable powder (WHO specification) was applied at an estimated rate of 20 lb. (10 lb. actual DDT) per acre as a 5 per cent. suspension of actual DDT.

There was an immediate drop in density of *G. morsitans* in this forest island. Little change was noticed outside it. The persistence of the deposit, which was clearly visible where new vegetation had not obscured it, was checked at 14-day intervals. Up to six weeks after spraying, examples of *G. morsitans* from unsprayed forest placed in contact with leaves or bark from the sprayed forest island died within three hours, while controls remained alive for 24 hours.

Preparation of area for full-scale spraying.

Regular weekly patrols were arranged to cover all the concentrations of fly in the area. A detailed map made from aerial photographs was prepared showing the watercourses and forest islands. These photographs were of inestimable value, for had it been necessary to make a detailed survey, the work would have taken at least an extra 12 months to complete. Motorable tracks were made so that supplies could be taken into, or near to, all the concentrations by Land Rover trucks, and paths were slashed around and through the forest islands to make spraying possible. It was planned that the spraying should take place during the second half of the dry season, when the fly would be most concentrated.

Application of the insecticide.

A dosage rate of 20 lb. of 50 per cent. DDT wettable powder, as a 5 per cent. suspension of actual DDT, per acre was attempted. However, it was almost impossible to assess the rate of application in practice and a visible cover of tree trunks and scrub was what was achieved.

Insecticide was applied in all the evergreen forest islands, using the paths slashed as a means of access to the interior. Attention was paid particularly to those parts shaded from direct sunlight and those less exposed to the scorching winds that blow at this time of year. In addition, intervening country was searched for minor tsetse populations based on some of the larger isolated thickets which could provide enough shade and shelter for a few tsetse. These populations were usually associated with tamarind trees and sometimes with *Mitragyna inermis*.

A significant proportion of the insecticide fell on the ground, although application was stopped before the insecticide started to run off. There was not much spraying of leaves, the vegetation being sprayed to a height of seven or eight feet only. It was originally planned to spray on the 5th March, 25th March and the 22nd April 1956, with weekly patrols to locate the areas where additional attention might be necessary.

In actual fact, with the equipment available, four to five weeks elapsed between the first and second spraying and the results were so good that no third application was called for. In the first application, 2,688 lb. of powder were used which was sufficient for 135 acres at 20 lb. per acre. Exact measurement was impossible but it was thought that the area of the forest islands which formed the concentration habitat was at least 200 acres; application was therefore less than

20 lb. per acre. This was not a satisfactory method of estimating dosage because the rate of application must depend on the type of vegetation being sprayed. In the second application, only 738 lb. of powder were used, largely because by this time everyone was more experienced in what required spraying. The second application was mainly to tree trunks; one part of the focus was not sprayed a second time, and in most cases the second application was necessary only for the control of *G. tachinoides*.

The effect on the population of *G. morsitans* as a whole, as revealed by the regular patrols taking in all the major concentration sites and some of the intervening country, was dramatic, as can be seen from fig. 3, which shows the histograms for two of these patrols. The flies persisted longest (5 weeks on round 3) in an area associated with *Mitragyna inermis*. The area was too diffuse to be sprayed in the same manner as the forest islands.

Concerning individual flies, nothing much was observed for 15–20 minutes, after which short bursts of flight, which became progressively more abnormal in

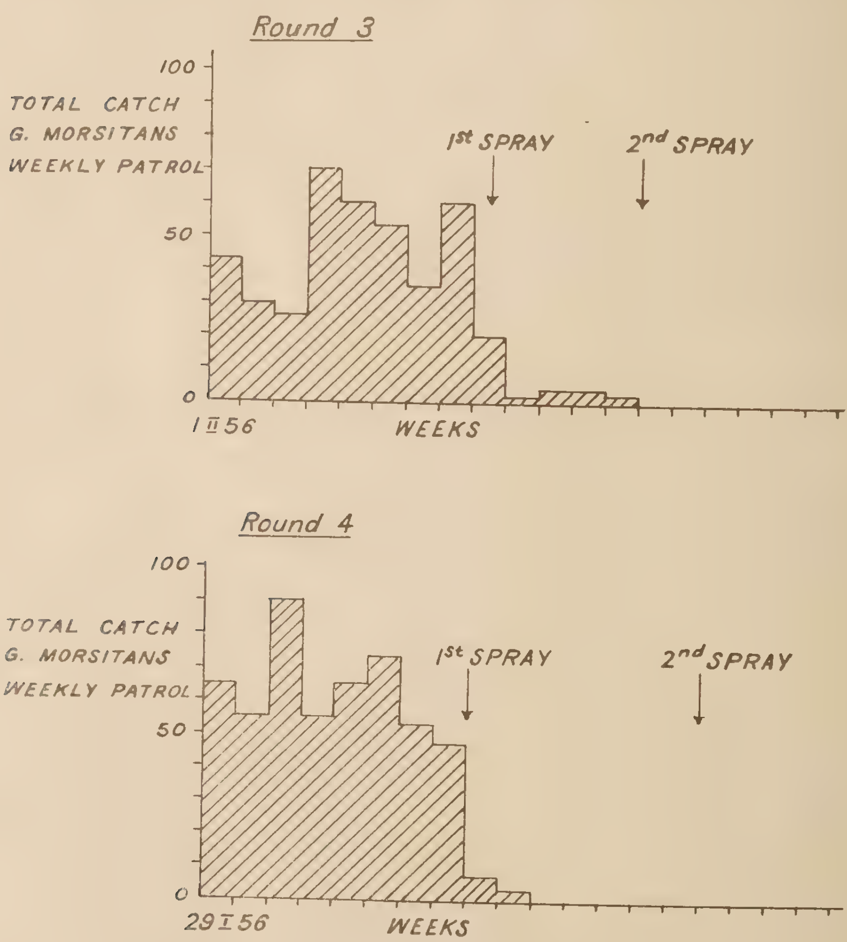

Fig. 3.—Catches of *G. morsitans* per weekly patrol before and after spraying.

character, alternated with spells of rest. There was little "washing" of wings and rubbing of legs at this stage. Later, loss of co-ordination, with periods of temporary recovery, ending in death after struggling with legs in the air, was observed.

During the wet season of 1956, it was not possible to keep the whole area under close observation but inspection of the margin of the seasonal inundation, where the flies used to accumulate, failed to reveal the presence of specimens of *G. morsitans*.

On the retreat of the seasonal inundation in October 1956, the area was carefully searched but no example of *G. morsitans* could be found. It has not been possible to find any specimens of *G. morsitans* in the sprayed area for up to 18 months after the last application of insecticide. The position regarding *G. tachinoides* is indefinite, due to the fact that, unlike the focus of *G. morsitans*, its distribution was continuous with the infestation on the river to the south.

A strictly comparable control was not arranged, but the population of *G. morsitans* on the same river, farther north, was under observation and maintained its density at the expected level at the time of the collapse of the population of *G. morsitans* in the sprayed area.

Discussion.

The method of eradication described depended for its effectiveness on almost the whole population of *G. morsitans* in the area spending at least a part of its life in the most favourable environment and on this environment being readily recognisable and forming a small portion of the whole area. Under such circumstances it appears that if sufficient of the concentration habitat has been treated with an insecticide with residual properties that remain effective for more than the length of the pupal period, the tsetse population will collapse.

It seemed probable that the concentration of *G. morsitans* along the paths cut round and into the forest islands, and movements of game and humans contributed to flies coming into contact with the insecticide. It also seemed probable that as the high density in the most favourable environment declined to a lower level, flies in less favourable outlying areas would more readily come in.

The fact that the treated surfaces were in the shade, and that the application was made during the season of no rain and at a time when vegetation was dormant, contributed to the good persistence noted. There may well be possibilities of economy resulting from a more detailed study of the dosage rate, persistence of the insecticide and of the tsetse resting haunts. DDT wettable powder has the advantage of low toxicity to man, visibility after application and the fact that extremely careful mixing to high rates of dilution and careful assessment of the rate of dosage are not essential to success. The best method of application of the insecticide may well be as a dust, but a simple, reliable and cheap machine must be available for this purpose. The penetrating power of a blown dust would be greater than that of the spray used. Poor penetration was a weakness in the method described.

When considering the possibility of extending the use of this method it is evident that it can be applied only after the retreat of *G. morsitans* to the forest islands in the second half of the dry season and before it disperses as the rains break. It is also necessary to treat all the foci of concentration in the whole area during this fairly short period of time and the area chosen must be isolated against the possibility of invasion from outside. The distribution of *G. morsitans* in the Sudan savannah zone of Kano, Bauchi and Bornu provinces of Northern Nigeria tends to be in linear strips associated with river flood plains and in which the fly lends itself to this type of attack. The situation is quite different in the Guinea savannah zone, where its distribution is more diffuse.

Summary.

The significance of *Glossina morsitans submorsitans* Newst. to the livestock economy of Northern Nigeria is mentioned. Differences in the ecology of the fly have been noted in the Guinea and Sudan savannah zones, respectively. In the former, its distribution is relatively widespread and diffuse whereas in the latter it is restricted to linear strips associated with river flood plains. The area dealt with in the present work lies in the Sudan zone. The relationship of the fly to its vegetational environment is described, there being a marked concentration of almost the whole tsetse population in evergreen forest islands of relatively limited extent in the second half of the dry season. The source of food is mainly wart-hog, which were numerous in the area.

A focus of the fly, covering an area of seven square miles, in which the dry-season concentration sites, mainly forest islands, amounted to approximately 200 acres, was selected for an experiment. It was isolated from the main focus by a natural barrier five miles wide.

Possible eradication measures in this focus are mentioned and reasons given for adopting the application of a residual insecticide.

DDT, in the form of a 50 per cent. wettable powder as a 5 per cent. suspension of actual DDT in water, was applied, during the second half of the dry season, at an estimated rate of 20 lb. per acre to the evergreen forest islands, which had previously had paths slashed around and through them. Pneumatic knapsack sprayers were used. A preliminary trial showed that, for up to six weeks after application of the insecticide, examples of *G. morsitans* from unsprayed forest, placed in contact with sprayed leaves and bark, died in three hours, controls remaining alive for 24 hours. It is suggested that this good persistence may be attributable to the fact that the treated surfaces were in the shade, and that the application was made during the rainless season and at a time when the vegetation was dormant. There was a rapid decline in the population of *G. morsitans* after spraying. The flies persisted longest (5 weeks) in a site associated with *Mitragyna inermis*. One application only was given to one part of the focus and in many others one application would probably have sufficed, the second being given in most instances to control *G. tachinoides* Westw., which was also present, and only in two instances for the eradication of *G. morsitans* that persisted after the first application. One of these was the site associated with *Mitragyna inermis*, mentioned above. The last specimen of *G. morsitans* was caught five weeks after the first application, and none has been caught in the sprayed area for up to 18 months after spraying. The cost of the insecticide and labour to apply it amounted to £700 for an area of seven square miles of focus in which the dry-season concentration sites to which insecticide was applied amounted to approximately 200 acres. The final result regarding *G. tachinoides* was indefinite for reasons which are mentioned.

Acknowledgements.

Acknowledgements are due to Mr. P. A. Nelson, Senior Control Officer on secondment from the Uganda Protectorate for the original survey of the area, to Mr. W. I. A. Dees, Senior Control Officer, for the preparation of the area and the implementation of the control. Acknowledgement is also due to Dr. S. G. Wilson, C.B.E., Director of Veterinary Services, for constant advice and for permission to publish.

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SOME MOSQUITOS OF THE BLUE NILE VALLEY IN THE REPUBLIC OF THE SUDAN.

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(Plates IV & V.)

Fifty five species and three varieties of Culicidae have been recorded (Lewis, 1956, and previous papers) from the Blue Nile valley in the Republic of the Sudan (fig. 1), and the present work deals mainly with three species of *Anopheles*, *A. gambiae* Giles, *A. rufipes* (Gough) and *A. pharoensis* Theo. Most observations were made in the Gezira at various times between 1935 and 1955, and at Sennar during visits between 1936 and 1940 and in a few subsequent years before 1951. Breeding conditions in the Sennar reservoir somewhat resembled those in the Jebel Auliya reservoir which were studied by Lewis (1948).

The following account does not show what happens every year in each locality because rainfall and river levels vary from one year to another, and control measures have produced great changes in some areas. Even where the breeding conditions no longer exist, however, a record of them is required for planning those anti-larval measures which are still necessary and those which might again be necessary in the event of mosquitos becoming resistant to residual insecticides.

As elsewhere in the Sudan, rainfall diminishes from south to north and mosquitos tend to do the same, but the natural conditions have been somewhat altered by irrigation, chiefly in the damming of the Blue Nile at Sennar and the watering of a large part of the Gezira plain (fig. 1), the country lying between the Blue and White Niles. The average rainfall, in mm., of several places on the Blue Nile is: Kiri, probably more than 1,000; Roseires, 808; Singa, 574; Sennar, 454; Wad Medani, 401; Khartoum, 163. Everywhere there is a long dry season. The country has been described by Tothill (1948) and by many other authors, so only a few relevant facts are mentioned below.

Records of numbers of larvae per square metre are based on series of sweeps with a net, each sweep covering about a fifth of this area. It was sometimes necessary to remove a little mud from the edges of pools and channels, and examine it in a dish of water, because larvae of *A. gambiae* were occasionally found in a thin film of water on the mud.

It will be found convenient, for this study, to divide the Blue Nile valley into the following sections: Kiri to Abu Hugar, Karkoj to Sennar, Sennar, the riverain area from Abu Geili to Soba, the Gezira irrigated area, Khartoum and "other areas". Each is considered separately in the following pages.

Kiri to Abu Hugar.

A considerable length of this part of the Blue Nile will become a reservoir when the proposed Roseires dam has been built at the Damazin rapids. Water will be stored each year from the beginning of September, when the water is heavily laden with silt, but scouring will be more active than in the Sennar reservoir and will remove much silt when the flood is rising (Sudan Government, 1954*a*,*b*). Our knowledge of the mosquitos above Roseires is limited to records

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* Care of the British Museum (Natural History). Formerly Entomologist, Stack Medical Laboratories, Sudan Ministry of Health.

of a few species from the rapids. Some of the water plants among which mosquitos breed in the Sennar reservoir are likely to occur above Roseires but conditions there are bound to be different owing to the different operation of the dam and the higher rainfall which is probably responsible for the common occurrence of *Anopheles funestus* Giles in this latitude.

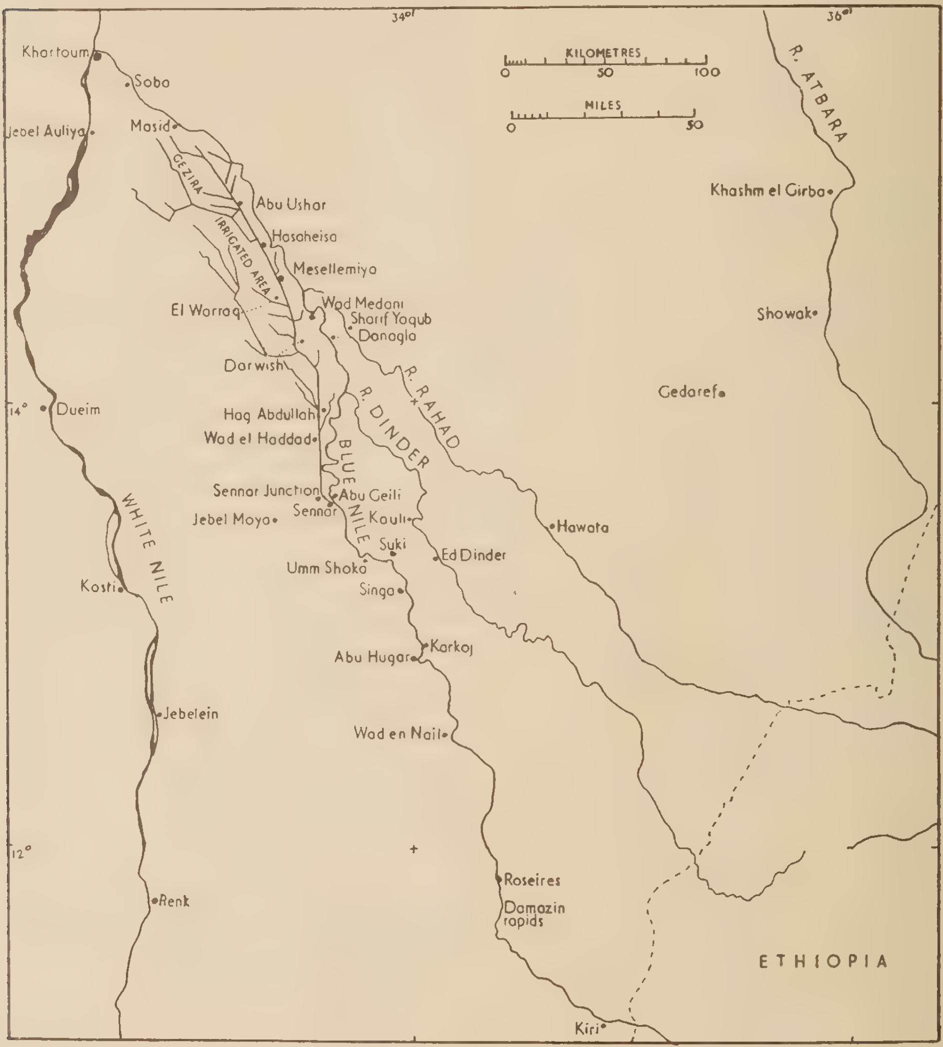

Fig. 1.—The Blue Nile and its tributaries in the Sudan.

An important feature of the Blue Nile from Roseires to Abu Hugar, and all the way to Khartoum, is a series of riverside basins or *maiya*, usually known as *sunt* woods or forests because the sunt, *Acacia arabica* Willdenow is the dominant tree in them. Kipling (1950) has described these basins, which have been formed from permeable silt, on the inner sides of meanders. At each bend in the 620 kilometres of river between Roseires and Khartoum is a basin covering between

about 100 and 1,000 feddans (a feddan being 4,200 square metres, about an acre). The basins are separated from the river by banks about the height of an average flood and are frequently inundated, naturally or by short canals. Sunt grows, or is grown, in them because it is the only local tree which, when young, can withstand up to three or four months of flooding. South of Sennar, where conditions are ideal for sunt (Booth, 1952), it is used for timber and the trees grow very large. Sunt has small leaves which cast scanty shade and often allow the growth of herbage in places where the ground is not flooded for a long period. The trees possess formidable thorns which can grow to a length of 66 mm. (2·6 in.). A grove of sunt presents an almost impenetrable barrier for the first six years of its life, or longer if the trees are badly watered, and even dead twigs can be a menace, sinking into the soft mud where they are a hidden trap for people wading.

A visit to the Roseires-Abu Hugar area in the rainy season showed that *A. funestus* occurred in several places. Abu Hugar, like Jebelein on the White Nile, appeared to be near the usual northern limit of this important vector of malaria, only a few individuals being sometimes found further north. The presence of the very similar *A. rivulorum* Leeson in the same area made it necessary to identify specimens of *A. funestus* with special care. In addition to these two, the ubiquitous *A. gambiae*, and *A. wellcomei* Theo., *A. pharoensis*, *Uranotaenia balfouri* Theo., *Ficalbia mimomyiaformis* (Newst.), *Culex poicilipes* (Theo.) and many other species were found in or near sunt basins.

Karkoj to Sennar.

The average monthly rainfall in mm. at Sennar is: April, 3; May, 24; June, 60; July, 119; August, 160; September, 70; October, 17; November, 1. The natural slope of the Blue Nile is about ten cm. per km. so the effect of the Sennar dam increases rapidly as one nears Sennar. Until 1950, the reservoir at full storage level had an effect on the low stages of the river as far as Abu Hugar and beyond, and on forest basins as far south as the Singa area (fig. 3).

Singa.

The reservoir did not affect breeding conditions during the rains, but its full storage level (figs. 3 & 4) was about two metres below the average maximum river level, with the result that the water in the lower part of a sunt basin did not drain away in November but persisted till about May. This area was flooded for so long that most of it was devoid of herbage and therefore unsuitable for the breeding of mosquitos. In the dry season the reservoir prevented the formation of natural residual pools in the lower part of the river-bed until May when it is usually so hot that little transmission of malaria is likely to occur.

A. gambiae bred in the very large flooded sunt forests during the rains, and continued to breed there in small numbers in marginal pools in the winter. The main body of water in these basins was not entirely free of mosquitos; for instance several fourth-stage larvae of *A. gambiae*, found in February in the Azaza basin below Singa, were in shallow water which had a clear surface except for a few small scattered sedge plants.

In recent years many areas between Singa and Sennar have been irrigated by pumps, and potential breeding places of *A. gambiae* have been created.

Thorough anti-larval measures are impracticable in the Singa area, mainly owing to the great extent of flooded sunt forest, and the obvious method of control is the use of residual sprays in houses.

Suki.

In this area, full reservoir storage level was about the same as the natural flood level, so that the water in sunt basins, after falling in September, October

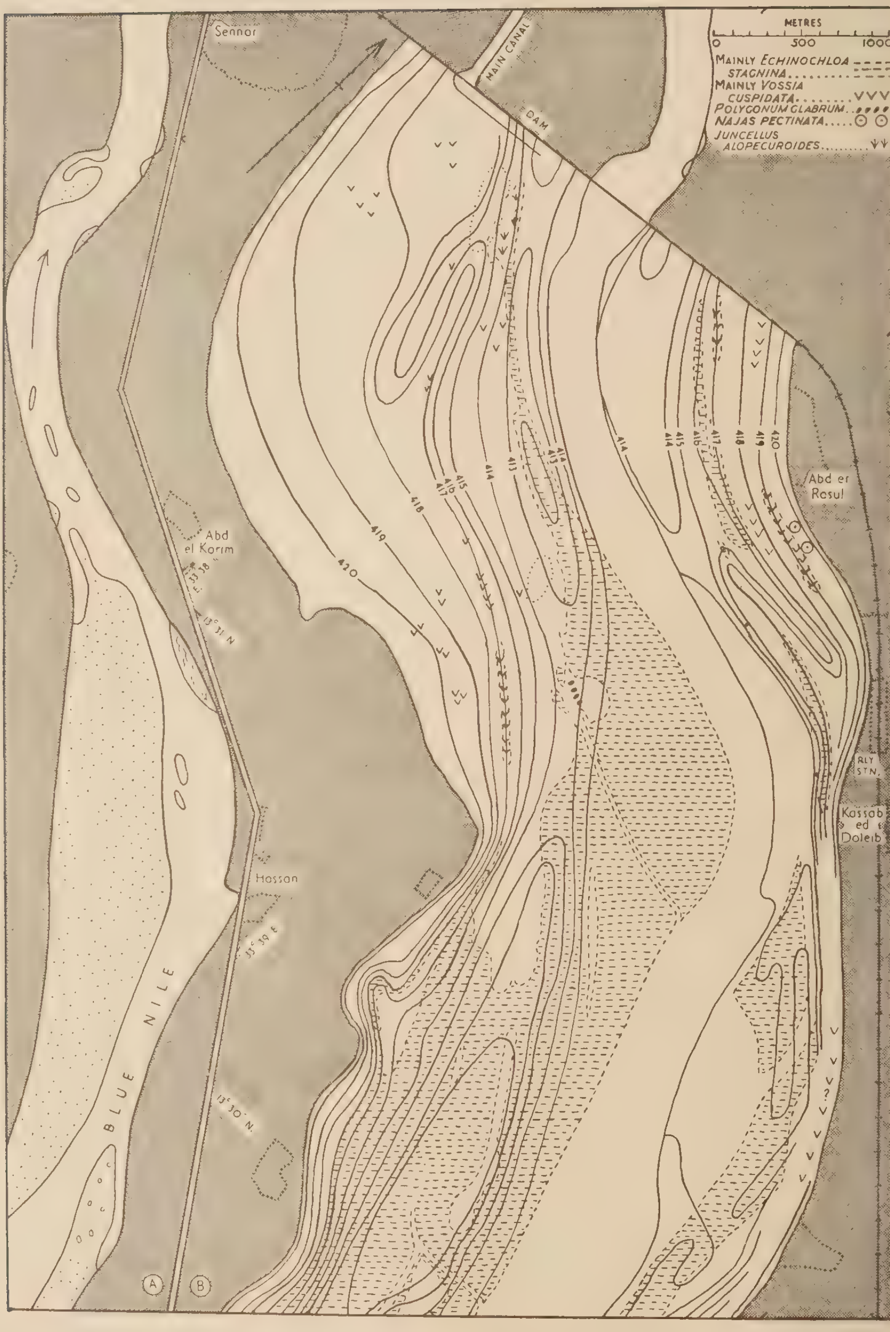

Fig. 2.—Showing (A) the Blue Nile at Sennar before the dam was built, and (B) pre-1925 contours, and the approximate distribution of water weeds in 1937.

and November, regained, through the manipulation of the reservoir level, its former height in the dry weather of December and remained high till February. The prolonged flooding killed many sunt trees, and *Echinochloa stagnina* (Retzius) Beauvois, *Vossia cuspidata* (Roxburgh) Griffith and other grasses grew thinly along the landward side of the inner banks of meanders.

In the basin opposite Suki, larvae of *A. gambiae* were found during February amongst the aquatic grass and in pools formed beneath uprooted trees and in hippopotamus tracks.

Umm Shoka.

In this area the maximum reservoir level was a little higher than the river banks so that, during full storage, there was a broad expanse of water broken by a narrow strip of floating grass which was anchored to the submerged inner bank of a meander (fig. 3).

Sennar.

In order to study the mosquitos of the reservoir, it was necessary to investigate the effect of reservoir conditions on water plants and the effect of these on breeding conditions.

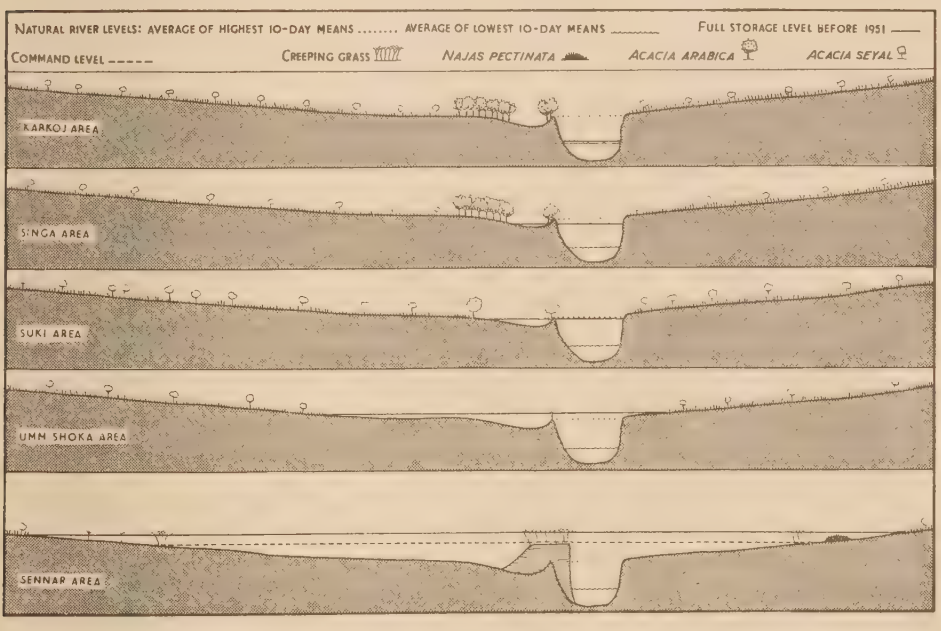

Fig. 3.—Diagrammatic sections of the Blue Nile showing the general effect of the reservoir on vegetation before 1951.

Control of Water Level.

The Sennar dam was planned to irrigate part of the Gezira (Anon., 1919; MacDonald, 1920) and its construction was completed in 1925 (Anon., 1924; Prowde, 1926; Russell, 1929). Allan & Smith (1948) gave an account of the working arrangements, and Hutchison (1953) recorded some recent alterations.

The dam has two purposes. It serves as a barrage to divert water into the canal which supplies the Gezira, and it dams up a store of water which is used for

watering the Gezira from February to April when almost the entire natural flow of the Blue Nile is allowed to pass down to Egypt. Deposition of silt has created a serious problem in many reservoirs (Taylor, 1930; Eakin, 1936), and the Blue Nile carries a heavy load of suspended material during the flood season. Arrange-

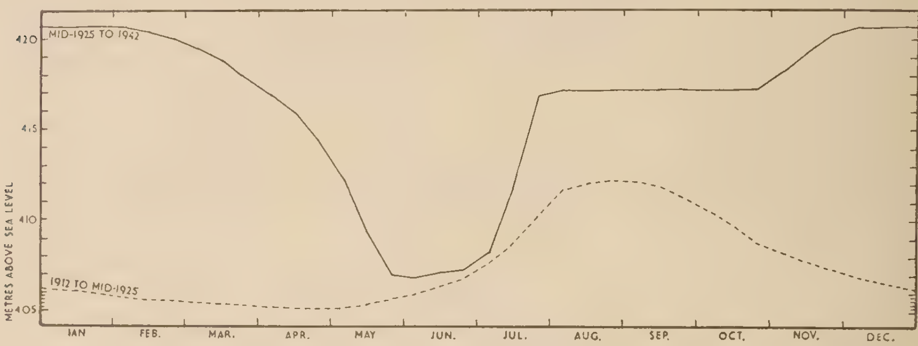

Fig. 4.—Water levels at Sennar before and after the dam was built: averages of ten-day means at the Makwar gauge (1·8 km. below the dam) and at the reservoir gauge, respectively.

ments were made, however, to reduce silting to a minimum by passing the flood-season discharge through the dam, much as is done at Aswan (Brown, 1943, p. 79), with the exception of a relatively small volume required to bring the water level up to 417·2 metres above sea level and so to command the Gezira main canal and divert water into it. Further storage was not to begin till the silt content of the river had become very small. MacDonald pointed out that the heavier particles of silt would travel in the trough of the reservoir, but that some silt would be deposited near the dam at the sides of the trough up to about 417·2 metres, and that in time this silting might conceivably extend as far as the 417·2 metre shore-line and up to a centimetre from the surface. This however would only destroy a fraction of the reservoir's full storage capacity most of which was to be carried between the 417·2 and 420·7 metre levels. MacDonald referred to the natural sunt basins in which some silt is deposited near the river but little in the hollows. A study of weed distribution in the reservoir showed that, in due course, a comparable process had occurred near Sennar, silt being deposited opposite Kassab ed Doleib in the form of a broad levee straddling the inner side of a meander (figs. 2 & 3) in an area which is referred to below as the main grass area.

Changes in water level (figs. 3 & 4) may be considered in relation to four annual periods, 15th July to 26th October, 27th October to 30th November, 1st December to 31st January, and 1st February to 14th July. On 15th July, adjustment of the water level began, and by 25th July it reached the 417·2-metre level which was then maintained. Between 27th October and 30th November the level was raised to full storage, which till 1950 was 420·7 m. (the highest level at which observations on mosquitos were made) and was afterwards increased by yearly stages to 421·7 m. From 1st December to 31st January the reservoir was usually full. It was emptied between 1st February and about 30th May, and remained empty till 14th July.

Water Plants.

Andrews (1945) and Tothill (1948) have recorded several species of water plants. During the present work the spatial and vertical distribution of some common species was studied by means of aerial photographs and soundings from

a boat. It is convenient to consider plant distribution in relation to three periods, 6th April to 25th July, 26th July to 26th October, and 27th October to 5th April.

About 5th April most water plants were stranded, including the two grasses, *Echinochloa stagnina* and *Vossia cuspidata*. Before the mud on which they grew could dry completely a little rain fell and kept them alive. The emptying of the reservoir enabled cattle to reach the grasses and graze on them, breaking the rhizomes so that they sprouted afresh.

From 26th July to 26th October, when the water was at command level, there were three shallow areas, two along the banks of the reservoir and a third, the above-mentioned main grass area, far from land. In August 1936, this area amounted to several hundred feddans and over much of it the water was between 15 and 80 cm. deep. A small area of mud was almost touching the surface in 1937 and had increased in 1938. *E. stagnina*, the more abundant of the two grasses, occurred in the main grass area and at other places just below command level, where, for nearly seven warm months of the year, it was either on damp silt or in shallow water. Between April and July the grass had been partly broken up and manured by cattle, and between July and October it was growing in a humid atmosphere engendered by the rainy season. Under these conditions it had a flexuous habit, like two species of the same genus in the Tennessee valley discussed by Hess & Hall (1945), and many stems grew horizontally over neighbouring plants to a length of nearly seven metres. *V. cuspidata* has very similar leaves but possesses characteristic large spiked glumes which are illustrated by Andrews (1956). Its habit and distribution were much like those of *E. stagnina* but it also occurred sparsely above command level in places where its rhizomes were not destroyed by weeding for cultivation when the reservoir was empty. During the command-level period the creeping grasses formed a dense mass in shallow water which was perfectly clear, in marked contrast to the turgid stream flowing swiftly past. This clarity, which was presumably favourable to mosquito larvae, was partly caused by the grass acting as a barrier and preventing silt-laden water from continually flowing in, rather as a species of tamarisk did in an American reservoir (Taylor, 1930; Brown, 1943). Presumably the water among the grass had originally been muddy and had become clear although, as Beam (1906) showed, the Blue Nile, during the rains, carries dissolved substances which cause clay particles to remain in suspension. He referred to the upper White Nile, where substances derived from decomposed vegetation cause clay particles to be precipitated, and it may be that precipitation among the grass at Sennar was due to a similar process. *Polygonum glabrum* Willd. grew in patches in relatively deep water at the edge of the grass area. When the water fell in the late dry season some of the *Polygonum* was burnt by herdsmen in order to protect the grasses for fodder. The giant sedge, *Juncellus alopecuroides* (Rottboell) C. B. Clarke, grew in very shallow water at the north tip of the main grass area in 1936.

From 27th October till 30th November, when the water was rising above command level, the leaves of the creeping grasses floated, and at full storage level the main grass area looked like an island but was an immense raft of foliage, rather sparse at first, moored by countless stalks in water about 3·6 m. or more in depth. The grasses now had a "floating mat" habit like that of the alligator weed, *Alternanthera philoxeroides* (von Martius) Grisebach, of the Tennessee valley, figured by Hess & Hall (1945). The dry weather of November had withered most of the grass growing on land above the water line, so that when the rising water created new shallow areas they were almost free of grass. The winter was relatively cold, but *Najas pectinata* (Parlatore) Magnus grew near Abd er Rasul in water which by then was clear. When the level fell in March this weed formed a spongy mass at the surface of water which was sheltered from the waves by the eastern strip of grass (figs. 2 & 3).

Echinochloa took several years to become established in the Jebel Auliya

reservoir, and the same was probably true of Sennar. According to local reports, the main grass area increased considerably between 1933 and 1935, and survived the November rise for the first time in 1936. From occasional observations since then it appears that the grass has not spread much farther. It looked rather sparse in 1952 (Pl. IV, fig. 1) after a season with the increased full-storage level, but Mr. I. A. Hutchison informs me that it survived the rise to 421·5 m. which made the depth in the main grass area about 4·4 m. in December.

Mosquito Species of the Reservoir.

Anopheles gambiae.

This species was much less abundant than the other two but its breeding places are discussed because it is an important vector of malaria. Near Sennar, it was liable to breed in rain-water pools and in scattered puddles at the edge of the reservoir. A few larvae occurred among *Juncellus* and many among *Najas*. Thirty three square metres of the latter were inspected in March and 78 Anopheline larvae were found to the square metre, most of them *A. gambiae*. *Najas*, however, was soon left high and dry, and it is unlikely that a short breeding period at this very hot and dry time of year led to much transmission of malaria. When Hassan village was examined during the 1939–40 season, adults first appeared at the end of August. They were numerous by the second half of November and were found in small numbers till the end of March.

Before the dam was built, the Sennar area was intensely malarious and *A. gambiae* abounded (Anon., 1926). During the construction period this species was controlled by measures described in the annual report of the Sudan Medical Service for 1925, and in later years the reservoir did not create any difficult problem as a source of *A. gambiae* near Sennar. Larvae in *Najas* were easily killed with paris green, and this plant could probably be controlled to a great extent by cultivation of crops and the use of poisons in the dry season.

Anopheles rufipes.

In both the Sennar and Jebel Auliya reservoirs, larvae of this species were found sparsely in areas overgrown with creeping grasses, and in considerable numbers in sheets of water without a thick covering of vegetation. Near Sennar, larvae were occasionally seen in the main grass area and some were found among *Najas* and *Juncellus*. Between 1936 and 1940, very few adults of *A. rufipes* were taken in houses. In January 1954, however, when many mosquitos were collected in villages between Umm Shoka and Sennar, this species was found to be common in some places and to outnumber *A. gambiae* in several. Further work is necessary to show if *A. rufipes* is always commoner upstream than at Sennar, or if it had increased in response to the raising of full storage level, which may well have thinned the raft of grasses and enlarged the area of *Najas*. Residual sprays used against *A. gambiae* probably kill many adults of *A. rufipes*.

Anopheles pharoensis.

Several hundred Anopheline larvae from the main and lateral grass areas were identified and almost all were found to be *A. pharoensis*. The exceptions were a very few *A. rufipes* and some *A. gambiae*, which once appeared when attempts were being made to destroy the grass. The number of square metres of grass examined and the numbers of larvae found per square metre were, respectively: in March, 28, 7; in August, 52, 11; and in October, 37, 11. Collections of adults on shore indicated that breeding in the grass diminished in late November and December, no doubt owing to the onset of relatively cold weather and the temporary thinning of the grass raft, when full storage level was first attained. Larvae of *A. pharoensis* were found in small numbers in the limited areas of *Juncellus* and

Polygonum, and many were once seen in a patch of *Utricularia* which had flourished as a result of removal of *Echinochloa*.

A. pharoensis and *C. poicilipes* were the commonest mosquitos found biting outdoors near the reservoir, 92 of the former and 113 of the latter being caught, for instance, in a few minutes on one occasion at Maiurno, a few miles upstream. The wind seldom blows from the reservoir to Sennar, so most collections of adults were made at Hassan village. As in Egypt (Bates, 1944) and on the White Nile, very few adults of *A. pharoensis* were found in houses by day in relation to the numbers present in the evenings. Observations at Hassan in the 1939–40 season, however, indicated that owing to local circumstances the adults sometimes remained near houses longer than they did in the Kosti area. Considerable numbers were found in four types of outdoor resting place, namely herbage near houses, shelters, known as *rakuba*, made of sorghum straw which were built on to houses after the harvest, herbage at the upper edge of the reservoir, and tent-like formations which were produced, about 700 metres from the village, when floating grasses sank with the falling water level in March and here and there became draped over sticks. Adults were seen in the waterside herbage from November till January and later. Herbage in the village was found to harbour some adults at the beginning of August, many in late August and early September, and some —in certain years—until the end of September, when the herbage dried up. Some were found in rakubas at the beginning of January, many in the first half of February, and some until the end of March. Adults were seen in the tent-like grass formations from the beginning of March till mid-April. To summarise, the annual cycle of events, as far as is known, was in general as follows: August and September, breeding active, many adults in village herbage; October to mid-November, breeding active, few adults found resting because herbage near the village had dried; mid-November to December, breeding reduced, some adults in waterside herbage; January to March, breeding increased, adults found in rakubas and waterside herbage, and in grass tent formations in March; April, breeding ceased, some adults in grass tent formations till mid-April.

Adults in houses were usually collected with suction catchers, and there was no indication that many sheltered in the thatch of roofs, but the possibility could be examined by the spray-catching method (Barber & Rice, 1938).

A. pharoensis caused much annoyance by biting. Owing to its markedly exophilic habits in the rather barren countryside of the northern Sudan, this species was not generally regarded as a malaria vector of much importance there. The observations on its resting sites at Hassan, however, indicated that it might perhaps play some part in transmission locally during February, August and September.

In 1935 and 1936, before a mosquito survey had been carried out, various attempts were made to prevent the growth of creeping grass. When the reservoir was empty, areas of the grass were poisoned, burnt, weeded by hand, ploughed or harrowed, and when the water was up, sections were cut out and pulled away by boats. Certain trees could have been planted with the object of killing the grass by shading but this would have added to the large amount of drift-wood which has to be collected to protect the dam. Arrangements to silt up weedy areas and dry them would have reduced water-storage capacity. The management of water level to control mosquitos, as practised in the Tennessee valley (Boyd, 1949), was not feasible at Sennar because changes of level would have interfered with irrigation requirements, raising the level in the command period would have caused silting, and fluctuations at a later date would merely have made the raft float up and down. The grass was checked to some extent by cultivators who rolled it up like a carpet in the dry season, and hundreds of tons were removed and sent away as fodder.

After a survey of the mosquitos had been made, attempts to control the grass

were discontinued. Not only was the work difficult and expensive, but it appeared to the writer that it entailed the risk of replacing *A. pharoensis* by much larger numbers of more harmful species. Interference with the grass would have left relatively open patches of water in which larvae of *A. gambiae* and *A. rufipes* would probably have bred, and the removal of shade would have favoured the growth of *Najas* or other submerged plants and the production of these two mosquitos in large numbers. Furthermore, destruction of the grass would probably have increased the deposition of silt and enlarged the area to be dealt with. Paris green, dusted from aircraft or boats as an experiment, penetrated the grass and killed the larvae but was not adopted as a routine measure owing to expense.

Measures are possible against adults of *A. pharoensis*, however, and should include the use of repellents, netting and screening, and residual sprays in rakubas, and the clearance of herbage and straw from the vicinity of houses.

Other species.

Becker (1923) visited Sennar in February 1914 and reported that *A. funestus* was numerous and annoying in a wood near the river and in his tent in the evening. During the present work, however, this species and *A. rivulorum* were usually conspicuous by their absence. It is possible that the species found by Becker was *A. rivulorum* and that both these mosquitos formerly existed at Sennar and have been displaced by the large population of *A. pharoensis* under the influence of reservoir conditions. Many examples of *C. poicilipes* bit in the evenings, and one was seen to bite at 1.15 p.m. in the main grass area. *Mansonia uniformis* (Theo.) and *C. antennatus* (Becker) were sometimes found biting.

Differences between the Sennar Reservoir and the Kosti Section of the Jebel Auliya Reservoir.

The Sennar reservoir is not far from the Kosti area and it is in the same latitude and has a very similar climate. In each area, *A. funestus* was common at about the same latitude, the same two species of creeping grass were dominant, and *A. rufipes*, *A. pharoensis* and *C. poicilipes* were prevalent.

There were important differences, however, between the two reservoir areas due to the Blue Nile having a considerable gradient and carrying a heavy load of silt in the flood season. The Blue Nile has eroded relatively steep banks so that it possesses no swamps in permanent contact with the main stream. As a result, papyrus (*Cyperus papyrus* L.) and the giant form of *V. cuspidata* were absent and there were fewer common water plants than on the White Nile, and no mosquito-eating Cyprinodontid fishes. Owing to the relatively steep topography, shallow swamps at the edges of the Sennar reservoir were not very extensive.

The seasonally abundant silt in the Blue Nile built up the riverside basins and had important effects on the reservoir. It formed the main grass area at Sennar, not as a lateral swamp like those at Kosti but as a submerged island. The isolation of the grass protected it from cattle for so long that in due course it formed a raft in more than 3·6 metres of water, as opposed to 1·5 metres or less at Kosti. Isolation prevented people from disturbing the grass and causing *A. gambiae* to breed in it. The suspended silt in the Blue Nile, by delaying the filling of the reservoir till the relatively cold dry season, caused the scarcity of vegetation—limited to very few common species—in the lateral shallow areas. Owing to this lack of diversity, there were fewer common species of biting mosquitos than at Kosti. Deposition of silt improved the soil (Tothill, 1948, p. 804) and encouraged people to cultivate in the dry season and so destroy the roots of some water plants. Owing to the abundance of herbage near houses at Hassan in the rains, *A. pharoensis* was evidently more associated with people there than it was at Kosti.

The Riverain Area from Abu Geili to Soba.

The sunt basins between Sennar and Masid covered a total area of some 12,000 feddans according to Kipling (1950). The basins varied in size and other respects and tended to be deeper south of Wad Medani. Much of the sunt north of Sennar was grown for fire-wood in a ten-year rotation, so plantations consisted largely of rather low, almost impenetrable, thicket. Most basins were flooded, naturally or intentionally, in July or August, at the height of the flood (Pl. V, fig. 1). The influx of water, supplemented by seepage and rain, formed lakes which persisted till October in many cases and could last till February at Danagla and till May at Deim el Masheika forest near Wad el Haddad. In many flooded forests one could distinguish three zones, the outer, middle and inner. The outer zone, which did not necessarily encircle the wood, included marginal pools and consisted mainly of shallow water overgrown with grass and to a varying extent with the small red-barked tree, *Acacia seyal* Delile, and small sunt trees (Pl. IV, fig. 2) which cast little shade. The middle zone, with relatively large sunt trees, usually contained little herbage, probably because the moderate shade of the trees prevented plants from growing high before the water rose. The inner zone, known as the *timta*, was about a metre or more deep and was usually flooded for so long that many water-lilies grew in it and little sunt or grass occurred. The sudden inrush of water at the beginning of the season created a large breeding place with very few predators. There were no Cyprinodontid fishes in the river and it took time for other species to enter and for insects to multiply. Probably for this reason, mosquito larvae have been seen swimming in open water in Danagla forest. This has also been observed near Singa, as mentioned above. As the basin dried, the predators were concentrated in residual pools in which one commonly found many examples of *Notonecta* and other insects but few mosquito larvae.

In the dry season the discharge of the Blue Nile shrank to about one-fortieth of what it had been in the flood, and residual pools formed in sand and mud and in a layer of calcareous rock which was exposed by erosion on the outer sides of meanders opposite the sunt basins (Pl. V, fig. 2). The sand pools, near the water's edge, were small and shallow and soon dried up but were more numerous than the rock pools.

Mosquito Species, Abu Geili to Soba.

Anopheles gambiae.

The annual sequence of breeding places varied from place to place but was in general as follows.

In August and September the outer zone of many sunt basins became an important breeding place of this species (Pl. IV, fig. 2), although grass-covered swamps elsewhere were usually free of *A. gambiae*. It is possible that the thorn trees, although not thick enough to prevent grass from growing, broke its continuity sufficiently to simulate pools. There were usually few mosquito larvae in the open water of the sunt and timta zones. Out of 472 Anopheline larvae collected in sunt basins, 49 per cent. were *A. gambiae*, 7 per cent. *A. rufipes* and 43 per cent. *A. pharoensis*.

In October, some larvae of *A. gambiae* were found in pools in forests. From October to April, or sometimes June, this species bred in rock pools and sand pools in the river-bed. The average number of larvae per square metre was higher in the rock pools and reached 45 in March of one year. In the dry season, nearly all the riverain Anophelines were *A. gambiae*, and all of 164 specimens identified from sand pools were of this species. Of 1,384 from rock and mud pools, 99 per cent. were this species and 1 per cent. *A. rufipes*, which was occasionally found in pools when its usual breeding places were dry.

From May to July, when the river was rising, very few larvae were found in sand pools, and none among rocks after June.

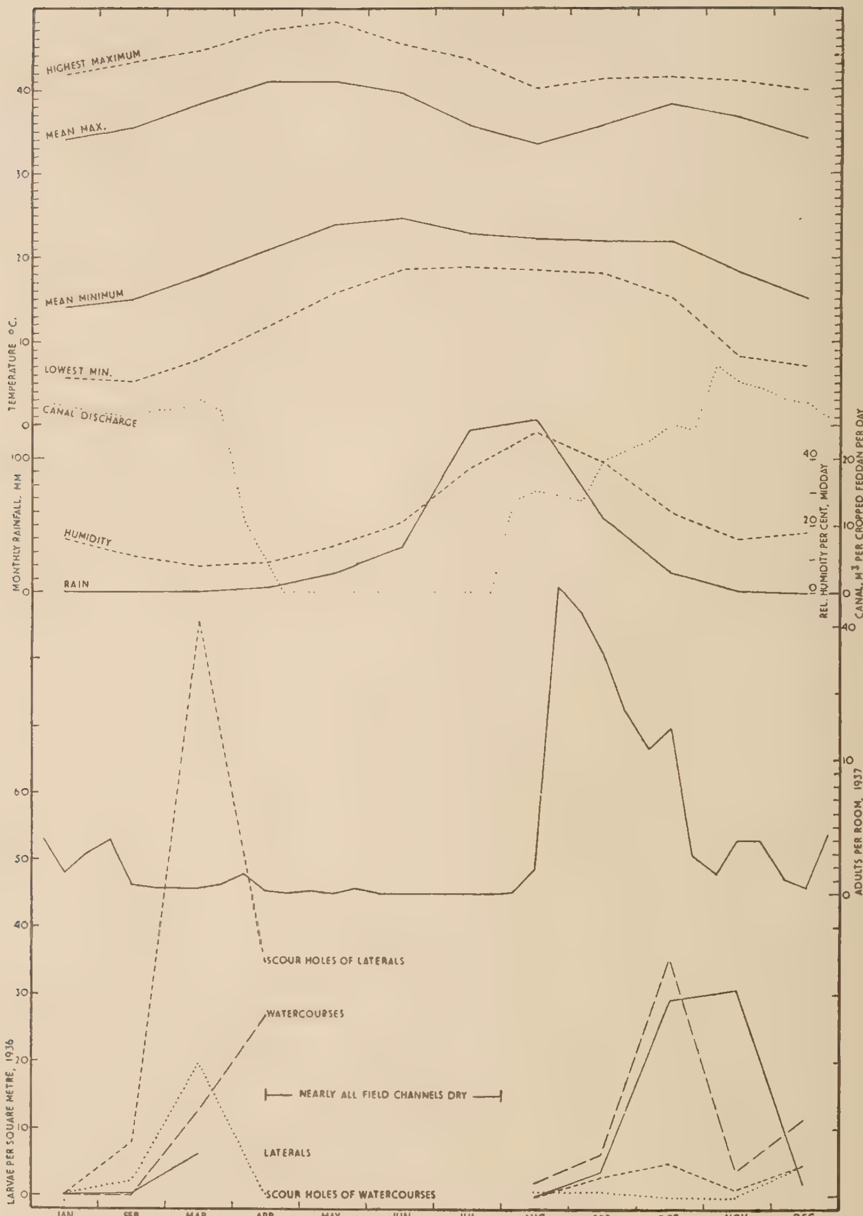

Fig. 5.—The Gezira irrigated area: average temperature and rainfall from 1921 to 1950, and average relative humidity at noon from 1925 to 1950, at Wad Medani; average discharge into the main canal, in cubic metres per cropped feddan per day, from 1935 to 1945 (after Tothill, 1948); average number of adults of *A. gambiae* per room in seven rooms in 1937; average number of larvae of *A. gambiae* per square metre in field channels in 1936.

It was difficult, for several reasons, to control larvae in sunt forests. The rain-soaked clay soil and flooded khors (seasonal watercourses) in the surrounding country often made access difficult in the flood season. Protective banks between the river and the basins would have been very costly to build, would not have prevented seepage and the entry of rain-water, and would have interfered with the cultivation of sunt, a valuable product in a dry country where wood is scarce. The height of the river prevented immediate drainage, but some basins were drained after a few weeks, and some partly drained to enable young trees to become established. Aerial application of larvicide would have been too expensive, and application from the ground was hindered by the trees which obstructed entry, and prevented effective dusting by cutting off the wind. In general, it was necessary in August and September to rely on residual sprays in houses, and afterwards to control larvae in a few basins which persisted for long periods near important places. Residual pools in the river-bed could be easily reached and treated.

Other species.

In addition to *A. rufipes* and *A. pharoensis*, mentioned above, larvae of *C. poicilipes* were common, and various southern species of mosquitos were found in sunt woods in some very wet years. For instance, larvae of *A. rivulorum* were once seen in Danagla forest, and *Toxorhynchites viridibasis* (Edw.) was once found breeding in a tree-hole near Wad Medani. One year, in September, 99 examples of *M. uniformis* and 19 of *C. poicilipes* were caught biting in a few minutes at Wad el Magdub forest, also near Wad Medani.

The Gezira Irrigated Area.

There are many descriptions of this area and its irrigation system (Anon., 1925; Johnstone, 1929; Andrews, 1945; Tothill, 1948; Lord, 1949; Greany, 1952; Beer, 1954; Hance, 1954; Ayad, 1956; and others). The mosquitos were studied after the beginning of various means of control which are mentioned below.

The weather, which was sometimes extremely hot and dry (fig. 5), and the peculiar nature of the soil had important effects on the ecology of the mosquitos. The country is almost flat and consists of an exceptionally heavy and almost impermeable dark cracking clay which was deposited as an alluvium when the climate was wetter than it is now. Impermeability naturally caused some water to remain on the surface, but several properties of the soil reduced the amount of standing water and so avoided difficulties which are met with in many other irrigation systems. Lateral seepage was so slight that the plots had no system of drains in which rain water would have stood. Banks of irrigation channels were nearly water-tight so water seldom seeped out of them to form pools, and it was unnecessary to use artificial lining like that used in some other systems (Henderson, 1952). Water applied to the surface of the soil did not sink down to the water table and cause it to rise and form swamps like those which are a serious problem in some schemes on light soil. Extensive cracks developed in the dry season. Under the eight-course rotation in force, large areas lay fallow for two years and there was time for the cracks to go deep, and some reached more than 1·5 metres (Lord, 1949). Such cracks help to drain the soil, and tend to reduce water-logging at the surface (Sreenivasan, 1942).

Types of Breeding Place.

Rain-water pools formed in field channels, at the edges of large rain-water floods, and occasionally elsewhere. These floods sometimes covered vast areas

and occasioned some alarm, but for the most part they were open wind-swept water, and a large part of their edges comprised the steep sides of irrigation channels.

The main canal was deep and almost entirely free from mosquito larvae. The large branches and the major distributaries seldom harboured larvae but some sections were at times overgrown with species of weeds which occurred in the minor canals. The numerous minors had a total length of over 3,000 km. Each flowed through one or more sluice gates which were closed every evening to store water when work stopped for the night. Each canal was therefore a small reservoir or series of reservoirs in which the level could fluctuate 30 cm. in every 24 hours. This system of night storage increased silting and the growth of weeds (Jones & Andrews, 1952) which comprised *Potamogeton perfoliatus* L., *Najas pectinata* and other species listed by Andrews (1945). Weeds were much less prevalent in the Abdel Magid area, in the north, where canals were deeper and flowed continuously (Stephenson, 1947). Water weeds in the Gezira were usually cleared, to allow free flow of water and to reduce the snail hosts of *Schistosoma*, before enough foliage reached the surface to shelter mosquito larvae. *Panicum repens* L., sometimes other grasses, and the sedge, *Cyperus rotundus* L., grew at the edges but were usually cut to a narrow strip.

The field channels consisted of watercourses and laterals. The former took off from the minor canals and averaged 1,400 m. in length, and each one flowed every 15 days or so, for about seven days at a time. They were normally kept free of sedge, but scour-holes formed near the inlet pipes.

A normal watercourse supplied ten laterals which looked like small watercourses and, between them, watered nine plots, each 280 m. long and 150 m. wide.

The plots growing cotton at any one time amounted to approximately a quarter of the total irrigated area of about a million feddans, and a much smaller fraction was sown with lubia beans. Sorghum was grown from August to October on about an eighth of the area. Unlike cotton, it was not sown on ridges so water tended to accumulate in low areas.

Water sometimes stood in escape channels leading from the main channel, in drains, and in a few places where water seeped from canal banks.

Mosquito Species in the Gezira Irrigated Area.

Anopheles gambiae.

Observations on breeding places began with monthly collections of larvae around Darwish and El Warraq and elsewhere in December 1935, and were continued in 1936, a very wet year in which the rainfall at Wad Medani in June, July and August was 54·3, 98·3, and 207·4 mm., respectively; 18,846 Anopheline larvae were found in 1,035 square m. of water examined in field channels, and others were collected in many other breeding places which were regularly visited. In 1937, in which year the rainfall in June, July and August was 26·6, 238·7 and 73·8 mm., respectively, seven isolated houses of irrigation watchmen were examined for adults each month (fig. 5). More examples of *A. gambiae* were found in them than in the same number of houses in villages, but fewer than in certain isolated huts near plots. In 1936, for instance, one of the latter yielded 25 adults on 4th October, 238 on 12th, 1,102 on 18th, 168 on 2nd November and 16 on 17th. Thousands of cotton pickers came to the Gezira in the early months of each year and lived in temporary huts near the plots, sometimes more than ten men sleeping in one hut. In a series of catches in 1938, over 400 examples of *A. gambiae* were found in one hut in January, but the maximum and average numbers fell in February and March. Although the catches of larvae and adults shown in fig. 5 were made in different years, subsequent observations have shown

that they give a useful picture of the situation as it was, and are used to support the general statements in the paragraphs which follow.

A. gambiae was by far the commonest Anopheline and, until about 1945, was almost the only species to be found resting in houses by day. Its prevalence throughout the year can conveniently be considered in six periods.

From 1st July to 25th August.—Most of the rain fell and irrigation began in this period, during which larvae of *Culex univittatus* Theo. and other members of the Culicini preceded those of *A. gambiae*. This species bred to some extent in scattered rain-pools, minor canals and field channels, but adults did not usually become numerous. This delay was attributed to several factors. From the earlier rain-storms, some water soaked into the upper 30 cm. of soil, and much ran down cracks; when the first muddy pools were formed, in soil which had been baked by the sun, these probably contained no algal food; and, after the dry season, there were few females to lay eggs.

From 26th August to 30th October.—This period of wet soil, rain, irrigation and warm damp air (fig. 5) was favourable for *A. gambiae*, and year after year the species multiplied at about the end of August. The very sudden increase of adults at that time in 1937, shown in fig. 5, was probably due to the heavy July rains in that year. During a period in September when the average air temperature was 31°C., eggs were placed in a net supported in a pool of water, and larvae, pupae and adults appeared 1, 6 and 7 days, respectively, after the first day. These, and other periods mentioned below, correspond roughly with those given by Holstein (1954). In October, larvae were particularly numerous in the watercourses of sorghum plots, and some occurred in the plots themselves.

From 1st November to 28th February.—Watering of sorghum had ceased. Larvae could always be found during this period but were not abundant because the relatively cold weather prevented many from maturing before field channels dried up after each watering. When the average temperature was 23°C., in November, eggs were placed in a pool as before and larvae, pupae and adults appeared after 2, 11 and 13 days, respectively. In December, at an average temperature of 20°C., the times were 3, 16 and 20 days.

From 1st March to 15th April.—The hot weather usually began in March, and numerous larvae, many in the third and fourth stages, were seen in the scour-holes of watercourses and laterals. Larvae were less numerous, and mostly very young, in the shallow pools along the courses of these channels (fig. 5) where the water dried rapidly. An increase of larvae at this season was noticed during other years in which collections were made, but no corresponding increase in the numbers of adults was observed, either in 1937 (fig. 5) or 1938, or in later years in which houses were examined. The discrepancy between catches of larvae and adults was attributed to the effect of the very severe atmospheric conditions on the length of life of the latter. The maximum shade temperature in March averaged nearly 40°C. and has exceeded 44°C., and the air was very dry. There were no shady river banks or dense woods, and the houses in which adults rested were of a simple type and became hot during the day. Females of *A. gambiae* have been found in holes in the ground and in cracks near the river, and it is likely that in the Gezira at this season a few females survived in cracks long enough for their eggs to mature. Probably not more could do so because near the villages, where mosquitos usually found their blood meals, most cracks were covered over by the tread of people and animals. Irrigation of the Gezira had created a situation in which, at this time of year, conditions were improving for the larvae just when they were deteriorating for the adults.

From 16th April to 30th June.—Irrigation had ceased and the temperature was known to reach 48°C. (118·4°F.). Even in the unusually hot summer of 1936, however, some females evidently survived long enough to lay eggs, for a few larvae

could be found in each month, in scattered pools in gardens and in the beds of drying canals.

Anopheles rufipes.

Out of 1,241 Anophelines caught in houses in 1936, 99·5 per cent. were *A. gambiae* and 0·5 per cent. *A. pharoensis.* In 1937 and 1938, *A. gambiae* continued to be almost the only endophilic species found, but in October and November 1946, *A. rufipes* was prevalent and continued in small numbers till the following March. Of 4,196 Anophelines, taken in various villages in that season, *A. gambiae* comprised 82·1 per cent., *A. rufipes* 17·2 per cent., and *A. coustani* var. *ziemanni* Grünb., *A. wellcomei* and *A. pharoensis* 0·1 per cent. each. The percentage of males was 11·6 for *A. gambiae* and 42·8 for *A. rufipes.* The percentage of females in the fourth or fifth ovarian stages was 52·9 out of 2,272 for *A. gambiae*, and 54·4 out of 334 for *A. rufipes.* Observations at Kosti (Lewis, 1948) had indicated that comparatively small numbers of *A. rufipes* remained in houses by day, and it was thought that these might be some females which remained for a short time after they had bitten. The high proportion of gravid individuals taken in the Gezira, however, suggests that there is some other explanation.

Anopheles pharoensis.

Larvae of this species have been found from July to November when the growth of grass in rain-water pools provided suitable conditions. In July and August, *A. pharoensis* bred in certain canals that had not been dried out and in which weeds had grown during the dry season before the river flood made the water muddy and the resumption of irrigation increased its speed. By November, larvae of this species were almost confined to a few canals. Some were found at times among sorghum straw which had been blown into canals.

Anopheles squamosus Theo.

Larvae of *A. squamosus* were found from August to October.

Culex univittatus.

This was the common representative of the Culicini but fortunately it rarely if ever bit man in this area.

The Importance of various Breeding Places.

Scattered rain-pools outside field channels were important for a short period and most of the Anopheline larvae in them were *A. gambiae.* In a collection of 77 larvae from this source, 70 per cent. were of this species, 23 per cent. were of *A. pharoensis*, and 7 per cent. were of *A. squamosus.*

Canals were not generally an important source of adult mosquitos and most of the larvae found in them belonged to species other than *A. gambiae.* Of 170 identified, 28·8 per cent. were *A. gambiae*, 2·4 per cent. *A. rufipes*, 57·6 per cent. *A. pharoensis* and 1·2 per cent. *A. squamosus.* Larvae of *A. gambiae* were seldom found among grass or sedge at the margins of minor canals, except in a few places where the vegetation was about a metre wide. In most places young larvae were probably swept away by the nightly rise of water level and killed by predators, but it is possible that a few reached field channels and continued their development. Larvae of *A. gambiae* were found among aquatic plants in a few places.

The great majority of larvae in field channels (watercourses & laterals) were of *A. gambiae.* The numbers of larvae identified were: January to April, total 1,120, all *A. gambiae*; August and September, total 171, 75·5 per cent. *A. gambiae*, 6·4 per cent. *A. pharoensis* and 18·1 per cent. *A. squamosus*; October and November,

total 699, 99·4 per cent. *A. gambiae* and 0·6 per cent. *A. pharoensis*. The many thousands of field channels (Pl. IV, fig. 3) looked very much alike but, at times, larvae were by no means evenly distributed among them, being more numerous around settlements and villages than in open country. In November 1936, for example, 52 pools in field channels within 5 km. of the Gezira Research Farm, near Wad Medani, were examined, 60 square metres being sampled, and 83·8 larvae were found to the square metre, none of the pools being devoid of larvae and 69 per cent. having more than 25 to the square metre. In open country, 62 pools—80 square metres—were found to contain 11·1 larvae to the square metre, 35 per cent. of pools being devoid of larvae and only 10 per cent. having more than 25 to the square metre. Sixty five pools—87 square metres—near two other settlements and within a kilometre of villages were examined and showed an intermediate condition.

Cotton plots usually dried quickly, and larvae were seldom found in them, but many were found at times in sorghum plots for a short period. Of 105 identified, 94 per cent. were *A. gambiae*, 4 per cent. *A. pharoensis*, and 2 per cent. *A. squamosus*. One might have expected to find more *A. pharoensis* in this situation, among herbage, but, owing to the spacing of the sorghum plants and the weeding of the plots, many of the pools were bare of vegetation.

Control of *A. gambiae*.

Usually, *A. gambiae* was the only common endophilic mosquito and the only species likely to transmit malaria. Henderson (1934) made a survey of the disease, and the annual reports of the Sudan Medical Service give accounts of its prevalence, and of control measures which are briefly summarised below.

Malaria formerly occurred throughout the irrigation period and increased immediately after seasons of heavy rain. In such years the number of cases multiplied in September and diminished in November and December, but continued to be numerous in certain mild winters.

Balfour (1913) foresaw the need for thorough control measures, long before irrigation began on a large scale. When this happened in 1925, a bailing system was instituted, by which cultivators were required, from 15th September onwards, to scoop water out of all field channels within three days of the end of each watering period. In the first year, leaky canals were a problem, but canal banks later became compact and leaks were usually unimportant. In the first few years, numerous borrow-pits were filled and a system of pumps and drains was installed to remove large bodies of rain-water from low areas. After a few years, oil was applied to scour-holes of watercourses, which were difficult to bail.

By 1935 much had been achieved, under a carefully planned system of intermittent irrigation and water disposal, but it was not enough to prevent the breeding of mosquitos described above. After 1935, larvicides were applied weekly to all rain-pools and field channels in a trial area round the Research Farm and in other limited areas. At first paris green was used, mixed with Blue Nile silt, a good diluent available in unlimited quantities. The arrival of DDT made it possible for a "mosquito-man" to carry a day's supply of cheap larvicide, a solution of DDT in Malariol or waste garage oil, in dropping bottles. After a time the use of larvicides was substituted for bailing which was slow, laborious and unpopular, exposed people to infection with schistosomiasis, and left many rain-pools untouched. Control was particularly necessary from about 20th August to the end of October, to check the rainy-season increase in Anophelines and to reduce the number of gravid females at the beginning of the winter, but it was difficult to obtain a large number of trained men for a limited period. Arrangements were therefore made for each cultivator to treat standing water in his own area, and good results were becoming apparent when large-scale residual spraying

began, all houses being treated twice yearly with BHC wettable powder, and malaria was much reduced.

Copper sulphate was used against snails in some canals at the rate of two parts per million of water (Sharif el Din & Jones, 1954). A preliminary inspection of the treated area in March 1954 indicated that some larvae of *A. gambiae* were dying as a result of this procedure, but the dosage was soon much reduced, and application limited to certain areas (Sharaf el Din & El Nagar, 1955).

Gambusia fish were useful in a few limited areas where small permanent water channels existed. It was impracticable to use plants to shade field channels, because they would have died when irrigation ceased (see p. 147).

The use of BHC in houses quickly became popular because it killed scorpions, as many as 22 in the roof of a single house, and soon afterwards its effect on malaria was widely appreciated. The absence of dense vegetation near houses and the trampling of soil cracks probably caused most adults of *A. gambiae* to rest in houses by day, but the hot climate reduced the period over which the insecticide was effective. The situation of the Gezira makes it particularly necessary to envisage the possible development of resistance to insecticides. Busvine (1957) pointed out that in Sokoto, where resistance has developed, hot, dry weather forced mosquitos into houses, and that this may have favoured the early development of resistance. Mattingly (1957) remarked that *A. gambiae* was living under relatively adverse conditions in Sokoto and that resistance might tend to appear first in the marginal part of its range or in a population established by man outside the natural range of the species. The Gezira is at about the same latitude as Sokoto and is near the northern non-riverain limit of *A. gambiae*, and for six months of each year the species is living there outside its normal range for that season.

Khartoum.

Anopheles gambiae.

This species, if not controlled, would breed in rain- and river-pools and in irrigation channels in the Khartoum stretch of the Blue Nile valley. It occasionally did so in part of the large sunt plantation south-west of the town, which was started in 1921 (Davie, 1924; Aylmer, 1931) to supply fire-wood. The plantation was actually on the White Nile but the Blue Nile banked up this river during each flood season and so controlled the flooding of the plantation. The average rainfall was so slight that little grass grew near the trees, and during the flood most of the water was too open to shelter mosquito larvae. When much rain fell early, however, a grass, *Brachiaria eruciformis* (J. E. Smith) Grisebach, and a species of jute, *Corchorus olitorius* L., grew among young trees in a seasonal watercourse at the north-east corner, and larvae of *A. gambiae* were found among them. Owing to the lack of silt in the White Nile, there was no bank between the trees and the river channel, so in due course, when the level of the White Nile fell, the water quickly drained away leaving only a few temporary pools in which *A. gambiae* was apt to breed for a short time.

Balfour (1904) reported that this species was the only Anopheline known in Khartoum, and described measures for its control. He (1906) recounted further measures, and later (1908, 1911) stated that they had been so effective that this mosquito was only occasionally seen. Boats were believed to bring a considerable number of mosquitos into the town (Balfour, 1903, 1909, 1910, 1912, 1913; Bousfield, 1919), and Balfour sprayed them with a pyrethrum solution, being one of the earliest to use pyrethrum in this way (Boyd, 1949). As a result of control measures, malaria became of minor importance in the urban area except in certain years of heavy rain. Suggestions have been made that the sunt plantation should be cut down, protected from flooding by an embankment, or drained by surface

drains after the flood. Drastic measures should not be necessary if the trees are cut back or thinned to allow of easy access to the breeding areas. This would make it easy to treat grassy areas and residual pools without the necessity for a drainage system which might hold up more water than the very shallow natural pools do.

Other species.

In this semi-desert region rain-water floods often consisted of sheets of open water with a few tufts of grass, in which most of the few Anopheline larvae present were of the innocuous *A. squamosus*. *Aëdes* (*Aëdimorphus*) *arabiensis* (Patton) often bred in these floods but fortunately does not bite man as far as is known. Many years ago, *Culex pipiens* L. was a pest in Khartoum, but in recent times it was only a minor nuisance in parts of Omdurman.

Other Areas.

The River Dinder.

A visit to Ed Dinder in December showed that the sandy river-bed was dry except for a few pools containing larvae of *Anopheles gambiae*. *A. rivulorum* has been found breeding in a riverside swamp at Kauli. *A. gambiae* bred in pools in the bed of the Dinder near its junction with the Blue Nile.

The River Rahad.

The bed of this river at Hawata was partly gravelly, and in the dry season many larvae of *A. rivulorum* and a few of *A. gambiae* occurred among pebbles at the water's edge. Near the neighbouring village of Hillet el Khalifa was a riverside basin in which *A. rufipes*, *A. pharoensis*, *Uranotaenia balfouri* and *Ficalbia mimomyiaformis* were found breeding in December. At the same time, *A. gambiae* bred in pools at Sharif Yaqub and near the mouth of the river.

Jebel Moya.

This is an isolated rocky hill west of Sennar on which *A. rhodesiensis* ssp. *rupicolus* Lewis, which is not known to bite man, and *Aëdes* (*Stegomyia*) *vittatus* (Big.) occurred.

Gedaref.

There is no permanent surface water in this area and the only Anophelines recorded are *A. gambiae* and *A. squamosus*.

Summary.

The rainfall of the Blue Nile valley diminishes towards the north, and the number of mosquitos tends to do the same, but the natural state of affairs has been somewhat altered by irrigation works in the shape of the Sennar reservoir and the watering of cotton, sorghum and sunt trees (*Acacia arabica* Willdenow), and will be further altered when the proposed dam at Roseires is constructed.

The latter dam will form a large reservoir in the Kiri–Roseires area where conditions are likely to differ from those of the Sennar reservoir. *Anopheles funestus* Giles and many other species occurred in the stretch downstream between Roseires and Abu Hugar in which riverside basins, overgrown with sunt trees, were flooded when the river was high.

Farther downstream, between Karkoj and Sennar, breeding conditions were affected by the Sennar dam, water at full storage level reaching different heights in the basins according to their distance from Sennar. Near Sennar the dual-purpose dam had a particular effect on the aquatic vegetation and the mosquitos.

A. gambiae Giles bred among *Najas pectinata* (Parl.) Magnus which, however, only occupied a small area in the reservoir, *A. rufipes* (Gough) bred in small numbers in various places, and *A. pharoensis* Theo. in a large area of creeping grass growing on silt under conditions which caused it to form a raft that rose and fell with the water. Adults of *A. pharoensis*, which was by far the commonest Anopheline, rested near houses by day at certain times of the year. Control of the grass was difficult and liable to favour more dangerous species of mosquitos. Differences between the Sennar and Jebel Auliya reservoirs are discussed.

In the riverain area between Abu Geili and Soba, *A. gambiae* bred in residual pools in the river-bed in the dry season and in flooded sunt basins in the rains. Control of larvae was very difficult in these basins and much reliance was placed on residual sprays against adults in houses.

Breeding conditions in the Gezira irrigated area are described with particular reference to the type of clay soil. There were many larvae of *A. gambiae* in field channels at the end of the rains when irrigation began, and in March when the summer started. The latter increase was not reflected by any increase in the number of adults, probably owing to the reduction in length of life of the latter in the very hot dry weather. *A. rufipes* was sometimes found in houses. Control measures are briefly described.

Some mosquitos of Khartoum and a few other areas within the Blue Nile valley are briefly considered.

Acknowledgements.

I am indebted to Dr. Mansur Ali Haseeb, head of the Stack Medical Research Laboratories, Dr. El Hadi el Nagar, Medical Officer of Health for the Gezira irrigated area, and successive medical officers of health and public health officers of the Blue Nile Province for help of various kinds; to the Sudan Ministry of Social Affairs for permission to publish Plate IV, fig. 1; to Mr. I. A. Hutchison for notes on the grass at Sennar after 1952; to Mr. P. F. Mattingly of the British Museum (Natural History) for reading the manuscript; and to Ahmed Effendi Abdel Rahman Bereir, Ahmed Eff. Ali Mohammed, Abdel Karim Eff. Abdullah and Osman Eff. Abdullah el Ramash, for their careful work as assistants.

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FIG. 1. Part of the Sennar dam and reservoir seen from the north-west in July 1952. The water level has risen to command the main canal which is seen in the foreground. In the middle background is the main grass area, and beyond the canal sluices is a dry area which is flooded during the full-storage period.

FIG. 2. A breeding place of *A. gambiae* at the edge of a flooded sunt basin near Wad Medani. The dense growth of young *Acacia* trees makes control difficult.

FIG. 3. A breeding place of *A. gambiae* in an irrigation watercourse near Wad Medani.

FIG. 1. The Blue Nile from the left bank at Wad Medani at the end of August when the average discharge exceeds 500 million cubic metres in 24 hours. A sunt wood is seen 600 metres away on the opposite bank, the inner side of a bend.

FIG. 2. The Blue Nile, from the view point of fig. 1, in April when the normal discharge is about 11 million cubic metres in 24 hours, and the river has fallen nearly nine metres below its flood level. A large pool in calcareous rock is seen.

THE EFFECT OF TEMPERATURE ON THE GROWTH RATE AND SURVIVAL OF THE IMMATURE STAGES OF *AËDES AEGYPTI* (L.).

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Several investigators have studied the effect of temperature on the growth rate of mosquitos (Bodenheimer, 1924; Headlee, 1924; Hurlbut, 1943, and others). However, very little work has been done on the effect of temperature on the rate of growth of the immature stages, and the only thorough investigation on the subject was made by Huffaker (1944) on *Anopheles quadrimaculatus* Say.

The purpose of the present investigation was to determine the effect of temperature on the growth rate and survival of each of the immature stages of *Aëdes aegypti* (L.). The amount of food available to the larvae is an important factor in determining the rate of growth (Trager, 1937; Bar-Zeev, 1957). The latter showed that, above a certain minimum, the amount of food had no effect, although when too much was given without renewing the water, a film of yeast formed on the water surface and caused mortality. In the following experiments, the food and water were renewed daily, the amount of food given being well above the minimum.

Materials and Methods.

The larvae were kept in flasks of water in incubators (60 × 38 × 39 cm.) within which the temperature was held constant (± 0·5°C.) by a bimetallic thermostat. A thermometer passed through the top of each incubator into the water containing the larvae. The temperatures tested were 14, 16, 20, 24, 28, 30, 32, 34, 36 and 38°C. The incubators themselves were kept in either a cold room (2–4°C.) or in an incubator room (28°C.).

When eggs of *A. aegypti* that are a few days old are placed in water, many larvae hatch from them within a few minutes. Four successive groups of such eggs were accordingly placed in water, with an interval of six hours between each, and from each group about 25 of the larvae that hatched within the first 10 minutes were collected and transferred to 100 ml. tap water with 0·3 g. bakers' yeast. in a 250 ml. Erlenmeyer flask, brought previously to the desired temperature. Each group of larvae was thus approximately six hours older than the following one. Six hours after the last group was hatched, and every 24 hours thereafter, the surviving larvae in each group were recorded and transferred to fresh water with yeast added, at the appropriate temperature, and the remaining exuviae recorded. The number of exuviae showed how many larvae in each group had reached the next stage since the previous examination. The average time at which any given stage was reached was taken as the mid-point of the six-hour period within which the number of individuals that had completed the previous stage reached 50 per cent. of the total that finally did so. Thus, supposing that in a group examined when 36 hours old, the 50-per-cent. point had been passed, and that in another group examined when 30 hours old it had not been reached, then the average time at which the given stage was reached was taken as 33 hours. The duration of any stage was taken as the difference between the

* Formerly Wolfinsohn.

TABLE I.

Duration and survival of immature stages of *A. aegypti* at different temperatures.

Temp. (°C.)	No. of newly hatched larvae	Larval stage												Pupa			T
		I			II			III			IV						
		N	H	%	N	H	%	N	H	%	N	H	%	N	H	%	
16	102	102	111	13·5	100	108	13·2	97	132	16·1	79	306	37·4	73	162	19·8	819
20	102	102	63	14·9	102	54	12·8	100	114	26·9	94	120	28·4	91	72	17·0	423
24	98	94	33	12·1	93	48	17·6	91	54	19·8	88	78	28·6	74	60	22·0	273
28	100	100	27	13·8	100	24	12·3	100	30	15·4	99	72	36·9	97	42	21·5	195
30	100	100	27	16·4	100	24	14·5	95	24	14·5	89	54	32·7	88	36	21·8	165
32	104	104	27	17·6	103	24	15·7	103	24	15·7	102	48	31·4	80	30	19·6	153
34	100	100	27	16·4	100	24	14·5	99	24	14·5	95	54	32·7	90	36	21·8	165
36	99	99	21	12·3	99	18	10·5	99	30	17·5	88	66	38·6	76	36	21·1	171
38	100	100 100*	27 —	— —	0 77 100*	— —	— —	0 100 100*	— —	— —	3 77 100*	— — —	— — —	0 0 68			

N = Number of individuals that completed the stage indicated.
H = Duration (in hours) of the stage indicated (for method of calculation, see text).
$\% = \frac{100\ H}{T}$
T = Average time (in hours after hatching) at which adult stage was reached.

* Larvae reared at 28°C. in this and earlier stages.

average times at which that stage and the succeeding one were reached. The same procedure was followed with each of the temperatures tested.

Results.

Results are given in Table I and fig. 1. The curves show the time required at the various temperatures for newly hatched larvae to reach the stages indicated. The horizontal distances between successive curves thus represent the duration of successive stages at the given temperature. The fourth stage was the longest

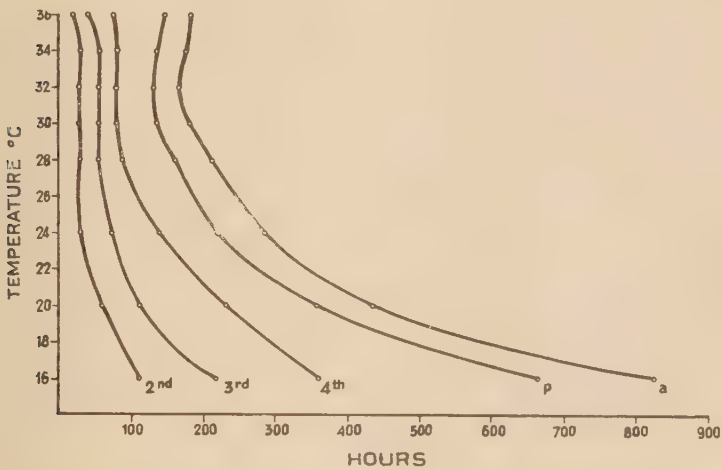

Fig. 1.—Time taken for newly hatched larvae of *Aëdes aegypti* to reach successive stages of development (2nd–4th, larval stages; P, pupa; A, adult).

(averaging 33·3% of the total time of development), followed by the pupal stage (20·6%), then the third (17·5%), first (14·6%) and second (13·9%).

Development from newly hatched larva to adult was most rapid at 32°C., but this was not so for all stages, development of the first and second stages being quickest at 36°C., and of the third at 30–34°C. There was no undue mortality at any of the temperatures examined, other than the extremes, 38° and 14°C.

Development at 14°C. was irregular and the mortality relatively high, and it was, therefore, not possible to determine the rate of growth of the individual stages. Only 24 per cent. of the larvae survived to the adult stage, of which half reached it within 60 days. At temperatures lower than 14°C., none of the newly hatched larvae was able to reach the adult stage.

The highest temperature allowing development of newly hatched larvae to adults was 36°C.; their growth at this temperature was slower than at 30–34°C.

At 38°C., all the newly hatched larvae reached the second stage, but none reached the third, and larvae reared to any given stage at 28°C. were, with few exceptions, only able to reach one further stage when brought to 38°C. (see Table I). The time occupied by each stage at this temperature could not be determined, as it is impracticable to obtain larvae just starting any given stage but the first. The mortality after transfer to 38°C. was determined every 24 hours, and is given in Table II. The fact that some larvae survived a week or more at 38°C. but reached only one further stage, indicates that at this temperature there is a cumulative injurious effect preventing further development.

TABLE II.

Survival of individuals of *A. aegypti* reared at 28°C. and transferred to 38°C. at different stages of development.

Time in hours	% survival after transfer to 38 °C. in given stage				
	I	II	III	IV	Pupal stage
24	100	100	100	90	97
48	95	88	100	63	68*
72	61	77	93	13	
96	39	61	91	6	
120	17	54	65	0	
144	4	43	39		
168	3	22	0		
192	0	16			
216		5			
240		1			
264		1			
288		0			

* All these pupae reached the adult stage within 72 hours.

Threshold of Development.

At sufficiently low temperatures, there appears to be a definite cessation of development. The threshold at which "on the descending scale development definitely ceases and at which on the ascending scale the development is initiated" (Uvarov, 1931), has been determined as follows.

One hundred larvae of each stage in 100 ml. of water with food given in

TABLE III.

Proportion of each stage reaching the next at low temperatures.

Temp. (°C.)	Stage	% reaching stage :				
		II	III	IV	Pupa	Adult
10	I	0				
	II		0			
	III			30·3	0	
	IV				2·7	0
	Pupa					0
11	I	0				
	II		6·7	0		
	III			83·0	0	
	IV				1·0	0
	Pupa					0·7
12	I	71·0	26·7	0		
	II		35·0	12·3	0	
	III			13·7	5·6	0
	IV				11·0	0
	Pupa					54·3
13	I	100	50·3	0		
	II		100	42·7	3·0	0
	III			88·3	10·6	0
	IV				86·7	18·0
	Pupa					90·3

At 9°C., none of the larval stages or pupae reached the next stage.

excess (2·0 g. bakers' yeast) were maintained at each of the following temperatures: 9, 10, 11, 12 and 13 (all $\pm$ 0·5) °C. The water, with food, was renewed every week, when the numbers of larvae and exuviae were determined. This was continued until all the larvae had died. Results are given in Table III, from which it is evident that the threshold of development lies between 9 and 10°C.

Discussion.

The relation of temperature to duration of development can be expressed by the formula

$$t(T-c)=K$$

where t is the duration of development, T the temperature, c the threshold of development (or more correctly the developmental zero, which does not necessarily coincide with the threshold of development), and K the thermal constant. The value of c can be obtained by plotting the reciprocal of time against the temperature. A straight line is obtained, if the time-temperature curve is a hyperbola (this does not take into account the extreme temperatures which are located outside the hyperbola). The developmental zero was thus found to be 13·3°C. (fig. 2). The threshold of development has been experimentally determined to

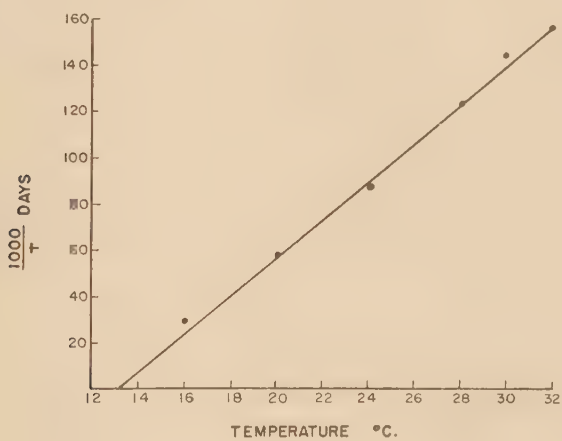

Fig. 2.—Relation between temperature and reciprocal of time taken by *Aëdes aegypti* to develop from newly hatched larva to adult stage.

lie between 9 and 10°C. and is, therefore, noticeably lower than the developmental zero. This is in agreement with results obtained with other insects (Peairs, 1927; Larsen & Thomsen, 1940).

By inserting the values of t (in hours) and c and T (in °C.) in the formula given above, the value of K was calculated for each of the temperatures tested:

Temp. (°C.)	14	16	20	24	28	30	32	34	36
K	1008	2211	2834	2921	2866	2755	2861	3415	3882

In accordance with results obtained by other investigators for many insects (Bodenheimer, 1955), the value of the thermal constant was found to be roughly independent of the temperature, except at the extremes (14 and 34–36°C.), and averaged 2,741 degree-hours between 16 and 32°C. The thermal constant for each stage separately, however, calculated from the values of t given in Table I,

was found to be temperature-dependent. That is to say, the curves obtained for the separate stages are not hyperbolic, but only the curve for the overall development from newly hatched larva to adult.

Growth of the first stage was most rapid at 36°C. The later the larval stage, the lower is the temperature at which growth is fastest. This may be because there is a cumulative delaying effect at high temperatures (as observed at 34–38°C., Table I). The more advanced the stage, the longer it is exposed to these high temperatures.

Summary.

The effect of temperature on the growth rate and survival of the immature stages of *Aëdes aegypti* (L.) was studied by rearing them at each of a series of constant temperatures from 14–38°C. in water to which adequate food (bakers' yeast) was added. Larvae were hatched, by immersing eggs in water, in four successive groups with an interval of six hours between each, and six hours after the last group hatched, and every 24 hours thereafter, those surviving in each group were recorded and transferred to fresh water and food, the exuviae remaining being recorded. The average time at which any given stage was reached was taken as the mid-point of the 6-hr. period within which the number of individuals that had completed the previous stage reached 50 per cent. of the total that finally did so.

The curve relating temperature and time of development from newly hatched larva to adult is hyperbolic, except at the extremes. The later the instar, the lower is the temperature at which growth is most rapid. The threshold of development was between 9° and 10°C., the developmental zero 13·3°C., and the average thermal constant (between 16° and 32°C.) 2,741 degree-hours. The highest and lowest temperatures permitting development from newly hatched larva to adult were 36° and 14°C., respectively. The average durations of the four successive larval stages and the pupal stage, expressed as percentages of the time taken for newly hatched larvae to reach the adult stage, were 14·6, 13·9, 17·5, 33·3 and 20·6, respectively.

Acknowledgements.

The writer is indebted to Professor Dr. F. S. Bodenheimer for his interest throughout this work, and to Mrs. H. Jordan for excellent technical help.

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RESPONSES OF PESTS TO FUMIGATION.

VII.—THE RELATION BETWEEN FUMIGATION TECHNIQUES, MORTALITY, AND THE AMOUNT OF HYDROGEN CYANIDE SORBED BY *CALANDRA* SPP.*

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Fumigation under reduced pressure has usually been recommended on the grounds that the fumigant would penetrate the commodity more readily when applied by one of the various methods of "vacuum fumigation". El Nahal (1953*a*,*b*) has shown that there is an important enhancement of susceptibility of the fumigated insects when they are exposed to low pressures, an increase which cannot wholly be predicted on the basis of their reactions to the fumigant or to the low pressures separately. When these two factors are combined, in a factorial experiment, the enhanced toxicity of the fumigant takes the form of a pressure-dosage interaction, as El Nahal has indicated.

There is not much information about the sorption of fumigants on insects, and still less about such sorption at reduced pressures. Lindgren & Sinclair (1944, 1945) recovered more hydrogen cyanide from resistant *Citrus* scale insects than from non-resistant insects. Similarly, more fumigant was recovered from the pupae of the Walnut Husk Fly, *Rhagoletis completa* Cress., when fumigated between 15 and 20 per cent. R.H. than when fumigated between 70 and 90 per cent.

Carpenter & Moore (1938) measured sorption of hydrogen cyanide on different species, and also found (Moore & Carpenter, 1938) that the sorption increased in fumigation at reduced pressures, although at the lowest pressure recorded (1–2 mm. mercury) sorption appeared to be reduced. This change has been discussed in more detail by Bhambhani (1956*a*). Pradhan & Bhatia (1951) measured both sorption of hydrogen cyanide and recovery of this fumigant from insects. The difference between these two quantities has been supposed to give a measure of the amount of fumigant metabolised by the insects.

The distinction drawn between the amount of fumigant applied, and the amount sorbed, or the amount metabolised, is a valuable contribution to the subject. The study of the availability of the toxic material to insects, which has proved a useful conception in work on contact insecticides, can now be extended to fumigations (Stringer, 1948). Unfortunately, the technique which Pradhan & Bhatia used for the recovery of the fumigant from insects has been shown by Bhambhani (1956*b*) to give incomplete recovery. In general, about half the unrecovered fraction which Pradhan & Bhatia discussed is in fact recoverable. The amount recoverable after short fumigation periods is so close to the amount sorbed that the difference between them is obscured by the associated experimental errors, although after longer exposures, of more than 4 hr., the irrecoverable fumigant can be clearly distinguished.

In the course of investigations reported in this series of papers, departures have been found from the simple rule that the product of the mean concentration and the period of exposure suffices to describe the biological effects of a fumigation.

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* Part of a thesis by H. J. Bhambhani approved for the degree of Ph.D. of the University of London.

Such concentration-time products, found by integrating the curve representing the changes of fumigant concentration throughout the fumigation, have served for many years to measure the effective dosage at any particular point within a chamber.

There are two main types of circumstance that seem to give rise to departures from this working rule. In the first place, a given concentration-time product is much more effective at low pressures than at atmospheric pressure (Salmond, 1953; El Nahal, 1953*a*), a discrepancy which cannot be accounted for by the mortality that arises at low pressures in the absence of fumigant (El Nahal, 1953*b*; Bhambhani, 1956*a*). El Nahal (1953*c*) found that hydrogen cyanide is sorbed more strongly on wheat in sacks if the fumigation is done at low pressures than at atmospheric pressure, even when full allowance is made for the greater concentration-time products obtained in the sustained vacuum fumigations.

TABLE I.

Treatments applied in a factorial experiment to investigate sorption of hydrogen cyanide on *Calandra* spp. at reduced pressures.

Factor	Levels chosen
Pressure (cm. mercury) ...	2, 27, 52 and 76 (atmospheric)
Concentration (mg./litre) ...	12, 26, 44
Exposure periods (min.) ...	30, 60, 90

TABLE II.

Treatments applied in a factorial experiment to investigate sorption on *Calandra* spp. of hydrogen cyanide at given concentration-time products made up in different ways.

Pressure (cm. mercury)	2, 37 and 76 (atmospheric)	
Concentration-time product (mg.hr./litre)	Time (hr.)	Concentration (mg./litre)
36	1	36
—	4	9
—	12	3
72	1	72
—	4	18
—	12	6
108	1	108
—	4	27
—	12	9

However, Page & Blackith (1954) showed that this result stems from the altered rate of penetration, the concentration being built up more rapidly in the sack: sorption on isolated grains is independent of the pressure. One object of the present paper is to present evidence to show that sorption is much heavier on insects at low than at normal pressures, thus offering a means of increasing the differential susceptibility of insects as compared with seeds.

In the second place, Salmond (1953) found that a given concentration-time product was less toxic when made up of long duration and low concentration rather than short duration and high concentration. El Nahal (1953*a*) found that consistently lower mortalities were obtained when insects experienced a concentration-time product inside a bag of wheat than when that same concentration-time product was attained around insects at the surface of the wheat in different experiments. Inside the mass of grain, the concentration builds up relatively slowly, whereas at the surface the insects experience the maximum concentrations attained soon after the gas is introduced.

Experimental.

The first investigation to be reported concerns the influence of low pressures on sorption. In a factorial experiment, the details of the treatments in which are given in Table I, both sorption of hydrogen cyanide and the mortality of the test insects (adults of *Calandra oryzae* (L.) and *C. granaria* (L.)) were measured and, in general, the two quantities showed similar changes as the experimental factors were varied. The methods of fumigation and estimation of sorption by

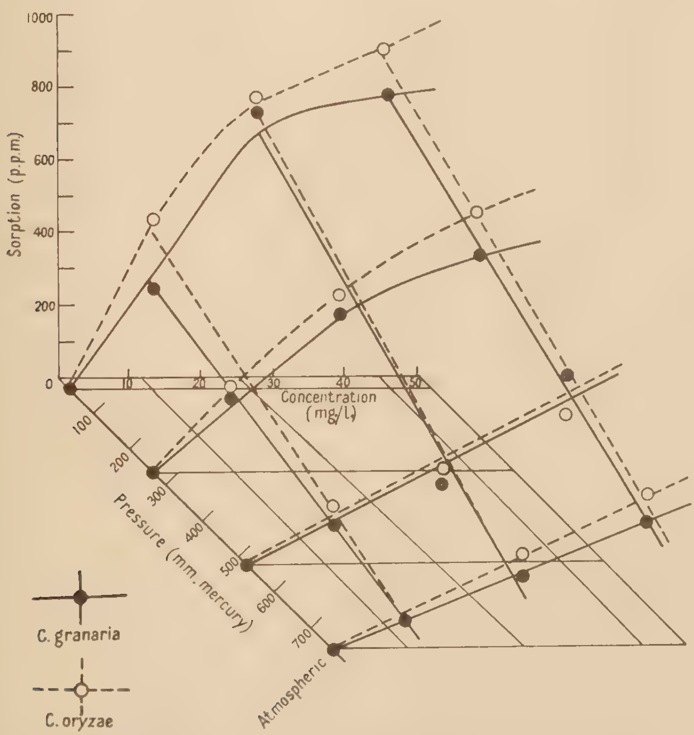

Fig. 1.—Sorption of hydrogen cyanide on *Calandra* spp. at different concentrations and pressures (after 90-min. exposure period).

recovery of hydrogen cyanide from fumigated insects, and the estimation of mortality, have already been described (Bhambhani, 1956*a*,*b*).

A further factorial experiment using the same two species of test insect was carried out on the relation between sorption of hydrogen cyanide and a given concentration-time product made up in different ways (Table II).

Since the concentrations of hydrogen cyanide applied were rather high, a complete kill resulted in many experiments. Attention has therefore been focused on the sorption measurements in this work, although useful information has also been gained from observations of mortality.

Results and Discussion.

In both species of *Calandra* much more fumigant is sorbed at reduced pressures (fig. 1), a fact of great importance in view of the greater toxicity of fumigants at low pressures (El Nahal, 1953*a*,*b*). At a pressure of 2 cm. mercury, about three times as much hydrogen cyanide is sorbed as at atmospheric pressure (fig. 2), and this difference must account for much of the marked interaction between pressure and concentration which El Nahal found. An interesting feature of fig. 1 is the greater sorption of hydrogen cyanide by *C. oryzae* than

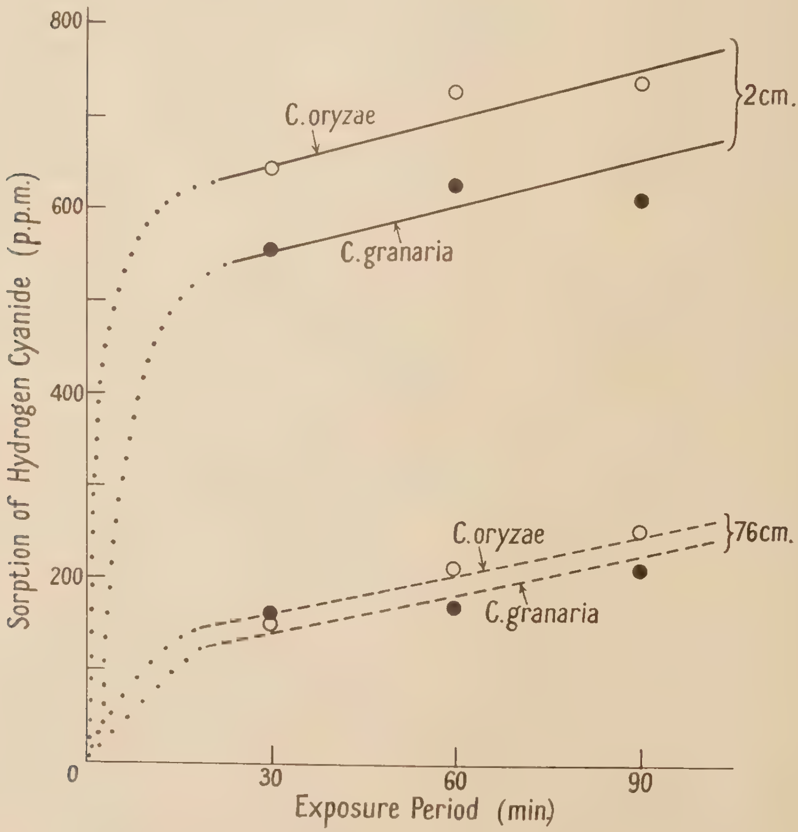

Fig. 2.—Rate of sorption of hydrogen cyanide by *Calandra* spp. (means of values obtained at three concentrations).

by *C. granaria* in this experiment, and an analysis of variance performed on the data confirmed the significance of this result.

As is to be expected, sorption on both species increases with the concentration of hydrogen cyanide. Increase of sorption also occurs with increasing duration of exposure (fig. 2) and it is interesting to compare this rate of sorption with that of a stored product (wheat) in which the insects are usually to be found. The rates of sorption in *Calandra* are linear, and Lubatti (1945) and Lubatti & Smith (1948) have suggested, in the case of plant seeds, that this is an indication that a slow chemical reaction is removing the sorbed fumigant, thus leading to the establishment of a "steady state". This situation is to be distinguished from that arising from mainly physical sorption, which can be described by a curve from which an asymptotic approach to equilibrium is apparent. An attempt to compare the magnitude of the sorption of hydrogen cyanide by *Calandra granaria* and by wheat is shown in fig. 3. The data for wheat are taken from

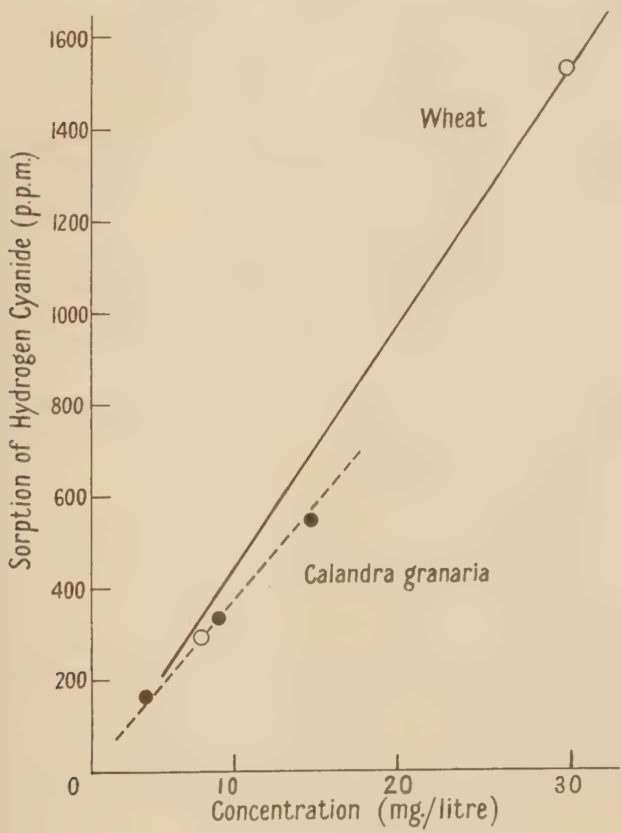

Fig. 3.—Sorption of hydrogen cyanide by wheat (treated for 48 hr.) and *Calandra granaria* (treated for 16 hr.).

Lubatti (1944), and those for the insect from a separate experiment made by one of us (H. J. B.), and no accurate comparison is possible because the shortest period for which data are available for wheat (48 hr.) is longer than the (16 hr.) interval for which the insects were fumigated. Nevertheless, the conclusion

seems to be justified that the relation of sorption to concentration is broadly similar in the two cases.

Details of the results of the second main experiment are given in figs. 4 and 5. In this experiment the effect of applying fixed concentration-time products, made up of differing components of time and concentration, was examined. A graph, similar to fig. 1, is shown in fig. 4, in which the exposure period was 1 hr. Results for the application of the same concentration-time products as in fig. 4,

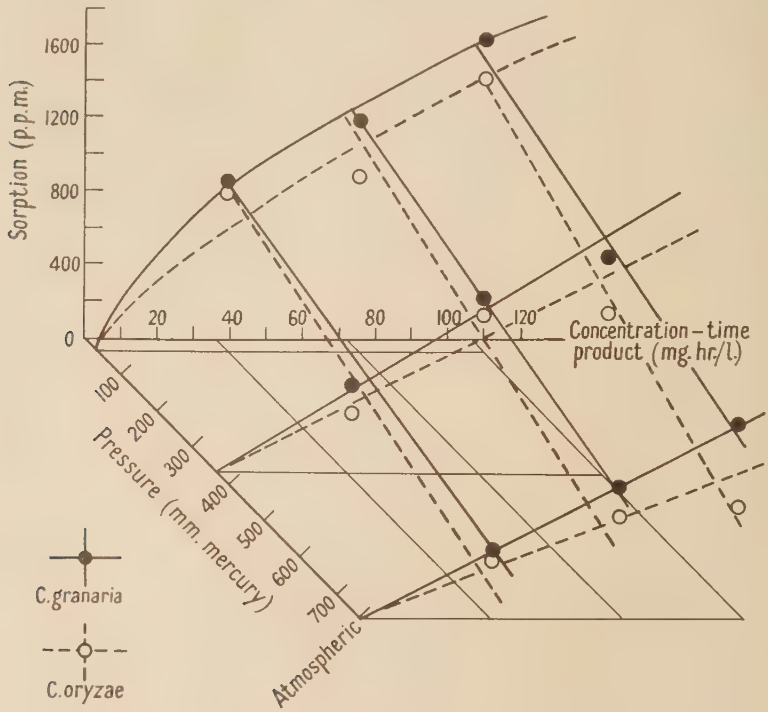

Fig. 4.—Sorption of hydrogen cyanide on *Calandra* spp. from concentration-time products with fixed short exposure (1 hr.).

but with a longer duration (12 hr.) are given in fig. 5. During this longer exposure, some of the sorbed fumigant may have been converted to products from which hydrogen cyanide is not recoverable. Two striking results with practical implications are evident when the two graphs are compared. First, for a given concentration-time product, the higher the concentration, the greater the sorption. Indeed, for both species, the sorption after 1 hr. is about double that arising from exposure to the same concentration-time product over a period of 12 hr. This conclusion is in agreement with that of Salmond (1953), and Lubatti (1945) demonstrated a similar phenomenon with wheat.

The second difference between figs. 4 and 5 was, however, unexpected. Analysis of the sorption data for the second main experiment revealed a markedly significant interaction between the concentration of hydrogen cyanide and the species of *Calandra* tested. Thus, whereas at high concentrations (36–108 mg. per litre) *C. granaria* was consistently more sorptive than *C. oryzae* (fig. 4), the reverse was the case at low concentrations (3–9 mg. per litre) (fig. 5). At an intermediate exposure-period (4 hr.) and range of concentrations (9–27 mg. per

litre), the two species sorbed almost identical amounts of hydrogen cyanide, so that the relative sorptive capacity of the two species was reversed according to whether the exposure was longer or shorter than 4 hr. The relative sorptive capacity shown in fig. 4 is, however, inconsistent with that shown in fig. 1 for comparable exposures and concentrations.

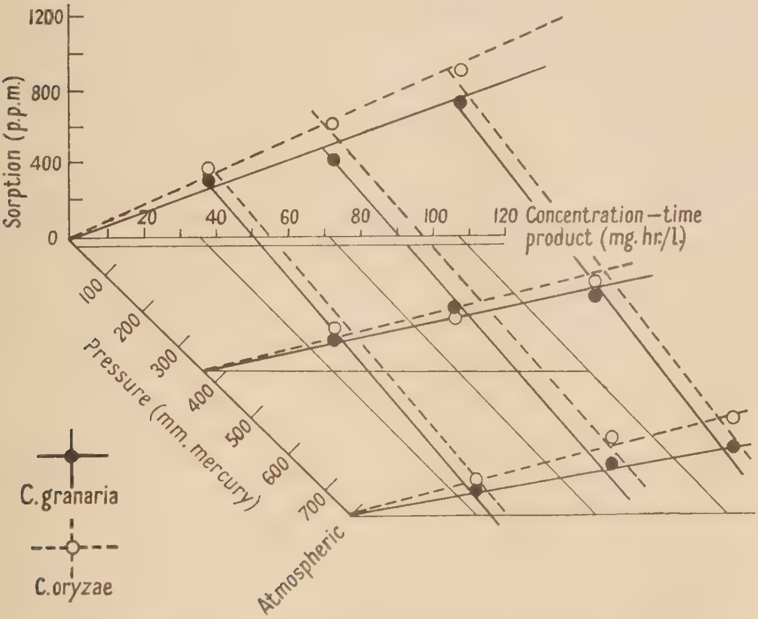

Fig. 5.—Sorption of hydrogen cyanide on *Calandra* spp. from concentration-time products with fixed long exposure (12 hr.).

The change of mortality with pressure, which is consistent with the associated changes of sorption, presents a particular difficulty of presentation. Analysis discloses a significant difference between the two species in the amount of additional hydrogen cyanide sorbed for a given pressure reduction, *C. oryzae* accumulating hydrogen cyanide faster than does *C. granaria* as the pressure is reduced, at least down to a pressure of 2 cm. mercury. However, the ratio of the sorption on one species to that on the other is remarkably constant, so that the interaction between species and sorption disappears if the analysis is carried out on the logarithms of the amounts of fumigant sorbed. This relation in biological assays is often found empirically to be substantially valid.

The quantity of immediate interest in practical fumigations is the mortality. The generally close relationship between mortality and the amount of toxic material sorbed by the insect has been established by Tattersfield (1927), Lindgren & Sinclair (1945), and Pradhan & Bhatia (1951). Salmond (1953) found *C. granaria* to be more resistant than *C. oryzae* to hydrogen cyanide at reduced pressures. Busvine (1942) found the reverse to be the case at atmospheric pressure. Our results suggest that this apparent conflict might be explained by the fact that the sorptive capacity of *C. oryzae* increases more than does that of *C. granaria* as the pressure is reduced.

Comparisons of species, as regards the mortality they suffer when fumigated, are thus only valid if account is taken of specific differences in sorptive capacity

under different conditions. At low pressures there is a striking, and as yet incompletely understood, association between sorption of fumigant, loss of water, and mortality. Grain weevils become considerably more active when the air pressure is reduced to about 2 cm. mercury, but at low pressures (1–2 mm. mercury) the insects become quiescent. Moreover, water is lost from the insects in a manner which varies with pressure as do physical activity and sorption of cyanide. The nature of the physiological change which suppresses sorption, dehydration, and activity at pressures below 2 cm. mercury remains obscure. Collapse of the insects' tracheae has been put forward as an explanation by Moore & Carpenter (1938), but there are several lines of evidence which render this explanation unlikely except as a very partial contributing factor.

Further quantitative comparisons of sorption and mortality are needed, at less severely reduced pressures or at atmospheric pressure, in which mortality from the action of low pressures will not dominate the experiments.

Data suitable for analysis are rare. Pradhan & Bhatia (1951) give measurements of the sorption of hydrogen cyanide on several species of insects, and mortality estimates for these fumigated insects are also recorded, in their Table IV. An analysis has been done on all these quantities with the exclusion of either zero or complete mortalities. Nine pairs of observations were available from adults of *Tribolium castaneum* (Hbst.), 11 from seventh-stage larvae of *Corcyra cephalonica* (Stnt.) and six pairs from adult females of *Drosicha* spp. Percentage mortality was transformed into angles prior to the analysis.

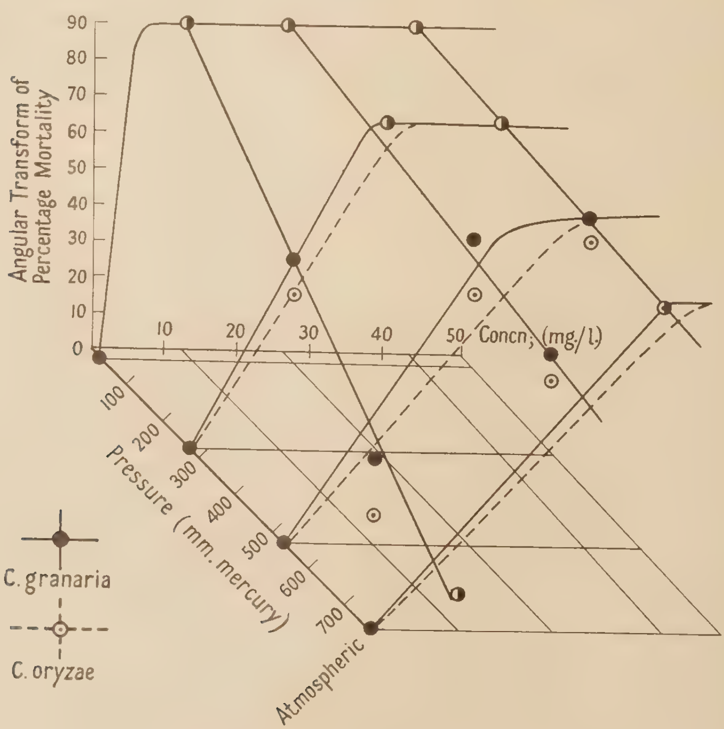

Fig. 6.—Mortality of *Calandra* spp. at different concentrations and pressures (90-min. exposure period).

The three species, which differed significantly in the mean amounts of hydrogen cyanide sorbed ($P<0\cdot001$), had been given doses estimated to produce equal mortality, and analysis disclosed no significant difference between the mortalities of the three sets of insects. This suggests that mortality differences between species are not wholly determined by the sorption of fumigant. A covariance analysis confirmed this suggestion. This result was to be expected on the basis of the hypothesis of Pradhan & Bhatia that the "total resistance" of a species is the sum of its "internal resistance" and "external resistance". Total resistance, measured by mortality, would on this basis vary between species to some extent apart from external resistance, as measured by the sorption of hydrogen cyanide. This "external resistance" recalls the availability coefficient of Stringer (1948).

Our observations of mortality are shown in figs. 6 and 7 for the longest and shortest exposure periods, respectively, in the first experiment. At 2 cm. mercury pressure, complete mortality was obtained almost throughout the experiment. The data obtained at this pressure were excluded from a covariance analysis that was made in order to compare the sorption and mortality. This analysis showed that, while the two quantities vary in much the same way with changes in the

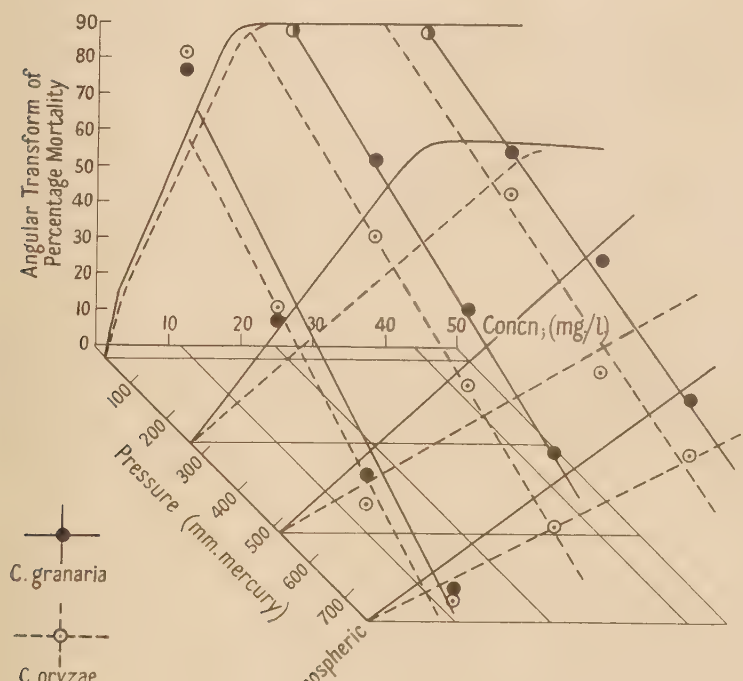

Fig. 7.—Mortality of *Calandra* spp. at different concentrations and pressures (30-min. exposure period).

conditions of fumigation, the increased mortality associated with increases in concentration are greater than would be expected from the associated alteration in sorption, and this discrepancy is significantly larger for *Calandra oryzae* than for *C. granaria*.

Summary.

The relation between fumigation techniques, mortality and sorption of fumigant was investigated by two factorial experiments in which adults of *Calandra granaria* (L.) and *C. oryzae* (L.) were exposed to hydrogen cyanide at concentrations of 12, 26 or 44 mg. per litre and pressures of 2, 27, 52 and 76 cm. mercury for 30, 60 or 90 min., or at given concentration-time products (36, 72 or 108 mg. hr. per litre), in each of which the time component was 1, 4 or 12 hr., and pressures of 2, 37 and 76 cm. mercury. The methods of fumigation and estimation of sorption and mortality were those used in earlier investigations and the results are shown in a series of graphs.

For both species, sorption of hydrogen cyanide increased as the total pressure was reduced, about three times as much being sorbed, in the first experiment, at a pressure of 2 cm. as at atmospheric pressure, the increase in sorptive capacity being greater in the case of *C. oryzae* than in that of *C. granaria*. In the second experiment, sorption by both species, for a given concentration-time product, was greater at a high concentration applied for a short period (1 hr.) than at a lower concentration applied for a long period (12 hr.); in the former conditions, *C. granaria* consistently sorbed more fumigant than did *C. oryzae*, in the latter, the reverse was the case, and in intermediate conditions (4 hr. exposure), the amounts sorbed by the two species did not differ materially. This result was inconsistent with that of the first experiment, in which *C. oryzae* sorbed more than did *C. granaria* during short exposures (30–90 min.).

These effects on sorptive capacity of differing conditions of fumigation could account for most of the reported departures from the rule that the biological effects of fumigation can be described by the product of the mean concentration of fumigant applied and the period of exposure. Comparison between mortality and sorption at pressures of 27–76 cm. in the first experiment showed, however, that while these were broadly associated, the increased mortality at higher concentrations was greater than would be expected from the associated increase in sorption, and this discrepancy was significantly larger for *C. oryzae* than for *C. granaria*.

Acknowledgements.

We should like to thank Professor Emeritus J. W. Munro for granting the facilities to enable this work to be begun, also Dr. A. B. P. Page, who supervised it, and Dr. O. F. Lubatti and Dr. F. Call whose valuable criticisms are greatly appreciated.

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THE RELATIVE SUSCEPTIBILITY TO PYRETHRUM IN OIL OF COLEOPTERA AND LEPIDOPTERA INFESTING STORED PRODUCTS.

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The object of this work was to determine the relative susceptibilities to pyrethrins in oil of a number of different kinds of insects infesting stored products. Laboratory tests were done on a wide range of species in their larval and/or adult stages, with a view to providing information useful in practical control. The value of such information has been discussed by Parkin (1953); with its help, control measures, especially against mixed infestations, can be better planned, and failures better accounted for. With practical needs in mind, the aim was to classify the kinds of insects into broad categories according to their susceptibility, rather than to obtain exact quantitative comparisons.

Solutions of 1·3 per cent. pyrethrins in heavy, highly refined mineral oil were used for many years in the control of stored-product insects in this country. This formulation has now been replaced by 0·3 per cent. pyrethrins plus 3·0 per cent. piperonyl butoxide, a formulation known to be about as insecticidal as 1·3 per cent. pyrethrins alone under certain circumstances (see Hewlett, 1951). Both formulations were included in the present experiments.

In the work described, the larval and adult stages of one species were regarded as different types of biological material, as distinct as insects of different species. Thus the term " type of insect " here signifies insects of one stage of a particular species, and the plural, " types of insects ", signifies a group of the larval and/or adult stages of one or more species. Scientific names refer to adult stages unless otherwise stated.

Materials and Methods.

Insects.

Most of the species were bred at 25°C., the remainder at 27° or 30°C.; all were bred at 70 per cent. relative humidity. For about half of the species used, the age of insects, the population density, the quantities of food, and the container size were well standardised for each species. For the remainder, these conditions varied considerably. The insects used in the tests were all taken from cultures that appeared to be healthy.

Previous experience indicated that examples of *Calandra granaria* (L.) and *Tribolium castaneum* (Hbst.) kept at 25°C. reach a maximum steady level of resistance to pyrethrum three weeks after becoming adult. Hence, adult insects normally living three months or more (which were all beetles), were exposed to insecticide when 3–5 weeks old. Shorter-lived adult insects were exposed when about half way through their normal span of life, in the hope that they would be neither so young as to be very susceptible to the insecticide, nor so old that many would die from natural causes in the course of an experiment.

Previous work (Campbell, 1926; Way, 1949; Mukerjea, 1953) has indicated that older larvae of a species are generally more resistant than younger larvae to insecticides, and preliminary tests of ours with larvae of *Ephestia elutella* (Hb.)

also suggested this. Larvae were therefore taken from cultures about a week before the first pupae were expected.

The insects were used in batches of 20–50, varying according to the type of insect, the number available, and the technique.

About half the types of insects were prepared for test as described by Parkin & Green (1943); batches of randomly chosen insects were put into glass jars (100 ml. capacity) with card footholds, and left overnight before treatment with insecticide. Insects capable of flying or climbing glass easily were not given footholds. Larger insects (*e.g.*, adults of *Tenebrio*) and cannibalistic insects (*e.g.*, larvae of *Tenebroides mauritanicus* (L.)) were put into jars (300 ml. capacity) with footholds of crumpled tissue paper. Insects with a short natural life (*e.g.*, moths, adult Bruchids) were taken from cultures on the day they were to be treated with insecticide.

Insecticides.

The insects were treated with two formulations, 1·3 per cent. w/v pyrethrins, and 0·3 per cent. w/v pyrethrins plus 3·0 per cent. v/v piperonyl butoxide (technical), in solution in Shell Risella Oil 17. The pyrethrin formulations and the oil will be referred to as P, P + PB, and R17, respectively. Applied as films, the two pyrethrin formulations were about equally toxic to *Tribolium castaneum* (Hewlett, 1951). In order to assist in interpreting the results, insects were also treated with R17 alone.

The pyrethrin solutions were made up on the day before use by diluting a concentrate containing 6·1 per cent. w/v pyrethrins as determined by the A.O.A.C. method (Horwitz, 1955, pp. 68–70). They were stored overnight at 20°C., and filtered just before use.

Application of the insecticides.

Except for moths, insects of each type were treated in two ways—by exposure to films and by direct spray; the moths were treated by the former method only. Where possible, the two techniques were employed as originally described (Parkin & Green, 1943; Hewlett, 1947*a*). The films were deposited on hard filter papers (Whatman No. 544) 7 cm. in diameter, and the insects were confined on them within glass rings 6 cm. in diameter and 2 cm. in height. While being directly sprayed, insects were confined in a metal ring 6 cm. in diameter and 0·8 cm. in height standing on a Whatman No. 1 filter paper. After treatment, the insects were swept into a clean glass ring standing on a Whatman No. 1 filter paper. In both techniques the insects were kept at 25°C. and 70 per cent. R.H. after treatment.

For the pyrethrin formulations the deposits (in mg. oil solution per sq. cm.) were as follows: film, 1·7, 1·9, 2·2, 2·5; direct spray, 0·30, 0·45, 0·67, 1·00. For the R17 oil alone they were as follows: film, 2·0, 2·5; direct spray, 0·35, 1·00. A total of at least 20, and where possible 50, insects of a type were exposed to each deposit of the three liquids in each technique.

The larger insects were directly sprayed in a glass ring 8·6 cm. in diameter and 2 cm. in height, and were confined in similar rings after spraying or while exposed on films. Where necessary, the rings were covered with pieces of wire gauze kept in place by weights.

Except for *Necrobia rufipes* (Deg.), insects able to climb glass were retained in the metal ring while being sprayed by a light smear of R17 on the ring (Hewlett, 1947*b*). None of the beetles tried to fly at 20°C., the temperature at which they were sprayed, although some could fly at 25°C.

Adults of *N. rufipes* were able to climb the oiled metal ring, and were therefore chilled, sprayed while immobilised, and swept into clean containers before they had time to recover. Pilot tests showed that pre-chilled individuals

of *C. granaria* were slightly less susceptible, and of *Tribolium confusum* Duv. slightly more susceptible, than beetles of these species treated by the normal direct spray technique.

Lids were put on the rings to confine glass-climbing insects after spraying or while on films. Each lid was a Perspex sheet with a hole covered by wire gauze.

Cannibalism and starvation.

If confined in groups, larvae of certain species, when pupating, affected by insecticide, or otherwise immobilised, were liable to be eaten by those more vigorous. In all but a few tests, cannibalism was prevented by confining each larva separately. A Perspex disc 4·5 mm. thick, pierced by seven holes 2·5 cm. in diameter, was placed on a sprayed filter paper 9 cm. in diameter. The disc was covered by a glass plate separated from the plastic disc by distance pieces of thin cardboard to allow ventilation. A larva was placed in each cell so formed.

Some species of beetles used, particularly *Oryzaephilus* spp., died rapidly when kept without food. In direct spray tests with such beetles, about 0·5 g. of food was put in each glass ring, one day after the introduction of the insects. The food was kept out of contact with paralysed insects.

Assessment of the effects of the insecticides.

The effects of the insecticides on the insects were determined as described by Hewlett (1947*b*). The insects were examined microscopically. An insect was classified as paralysed if it lay on its back unable to regain the normal position, or was unable to co-ordinate its movements when disturbed. An insect was counted as dead if it neither moved spontaneously nor responded by reflex movement to pressure with a soft brush, or, if a larva, to slight pressure with a blunt probe.

In tests with larvae, the insecticide frequently upset pupal development, so that some pupae failed to respond in any way when touched or lightly pressed with a probe. Even if there was no response, pupae which appeared to be perfectly formed and free from damage were recorded as alive; but any pupa showing extensive cuticular collapse, or other distortion, was recorded as dead.

Insects were examined 3, 6 and 9 days after being directly sprayed or placed on films: with very susceptible insects a 1-day count was done also. An examination is referred to as the 6-day count, etc.

Whenever possible the insects were examined *in situ*, only the dead being removed; disturbance of the insects was thus kept to a minimum.

Some larvae spun cocoons out of contact with the insecticidal films. These cocoons, containing larvae or pupae, were gently detached and placed on the films.

Results.

Analysis.

So that the results could be readily appraised, certain data were entered on a chart for each type of insect. Fig. 1 shows a typical chart. The histograms indicate control mortalities, and mortalities, corrected for control, produced by the oil and the pyrethrum formulations. The blocks of each group represent the percentage mortalities for the respective deposits (see p. 178).

The types of insects varied widely in their susceptibilities. For example, at six days, all the treated examples of *Sitotroga cerealella* (Ol.) were dead, but none of the larvae of *Tenebroides mauritanicus*. Superficial inspection of the charts sufficed to place the types of insects approximately in order of susceptibility; but they were placed more accurately by summing the 6-day mortalities of the pyrethrum-treated insects of a type from film and direct-spray tests. This was

TABLE I.

Types of insects* grouped according to their susceptibility to pyrethrins, and pyrethrins *plus* piperonyl butoxide, in oil.

Very susceptible	*Sitotroga cerealella* (Ol.)	
	Latheticus oryzae Waterh.	
	Ephestia elutella (Hb.)	
	Ephestia cautella (Wlk.)	
	Necrobia rufipes (Deg.)	
	Calandra granaria (L.)	
	Acanthoscelides obtectus (Say)	
	Callosobruchus chinensis (L.)	
Susceptible	*Caryedon fuscus* (Goeze)	
	Anagasta kühniella (Zell.)	
	Stegobium paniceum (L.)	
	Oryzaephilus mercator (Fauv.)	
	Latheticus oryzae Waterh.	larvae
	Oryzaephilus surinamensis (L.)	
	Trogoderma versicolor (Creutz.)	
Moderately susceptible	*Calandra oryzae* (L.)	
	Oryzaephilus surinamensis (L.)	larvae
	Tenebrio obscurus F.	
	Rhizopertha dominica (F.)	
	Oryzaephilus mercator (Fauv.)	larvae
Moderately resistant	*Lasioderma serricorne* (F.)	
	Ephestia elutella (Hb.)	larvae
	Tenebrio molitor L.	
	Alphitobius laevigatus (F.)	larvae
	Tenebrio obscurus F.	larvae
	Tribolium castaneum (Hbst.)	larvae
	Tribolium castaneum (Hbst.)	
	Gibbium psylloides (Czenp.)	
	Gnathocerus cornutus (F.)	
	Ephestia cautella (Wlk.)	larvae
	Alphitobius laevigatus (F.)	
	Tribolium confusum Duv.	larvae
	Ptinus tectus Boield.	
Resistant	*Ptinus tectus* Boield.	larvae
	Stethomezium squamosum Hinton	
	Niptus hololeucus (Fald.)	
	Tenebrio molitor L.	larvae
	Gnathocerus cornutus (F.)	larvae
	Anagasta kühniella (Zell.)	larvae
	Tribolium destructor Uytt.	larvae
	Trogoderma granarium Everts	larvae
	Tribolium confusum Duv.	
	Tenebroides mauritanicus (L.)	
	Mezium affine Boield.	
Very resistant	*Tribolium destructor* Uytt.	
	Dermestes lardarius L.	larvae
	Dermestes lardarius L.	
	Tenebroides mauritanicus (L.)	larvae

* Adult stage unless otherwise stated.

justifiable, because the same set of doses was used for each type of insect, though clearly the procedure was a rough one. For many types the data did not allow LD50's to be obtained.

The above procedure placed the types of insects in the order shown in Table I, after which the list was split into the groups indicated—very susceptible, susceptible, moderately susceptible, moderately resistant, resistant, and very resistant. Table II shows the mean 6-day mortalities for the insects in the different groups (the other data in the Table are referred to later). The summing of the mortalities probably makes the groups towards the extremes cover wider ranges of susceptibility, as judged by LD50's, than those in the middle of the series.

Various special aspects of the results are now considered.

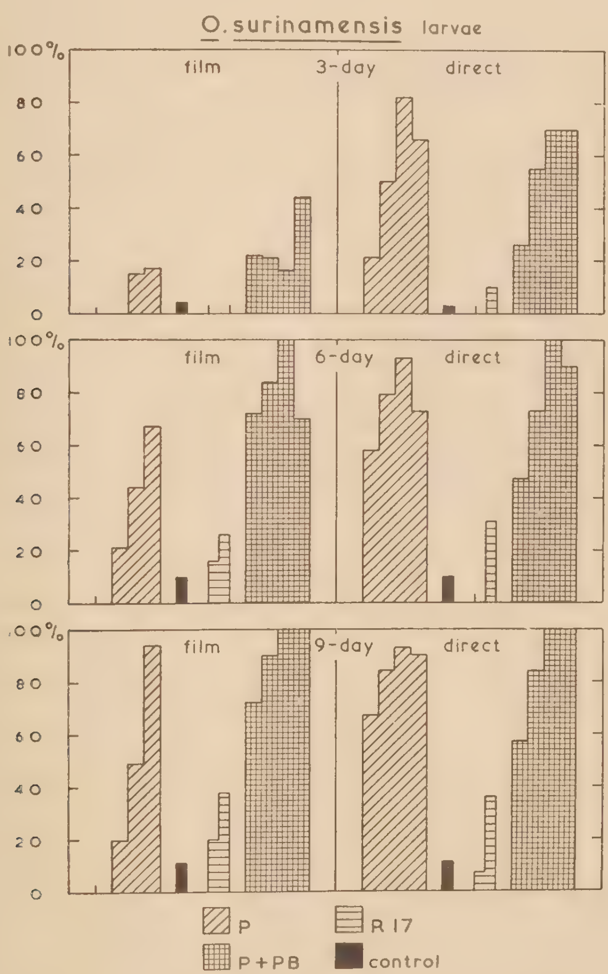

Fig. 1.—An example of the charts used to assess experimental data, in the determination of relative susceptibility. The steps in the histograms show the percentage mortality at different dosages.

Control mortality.

Heavy control mortality (more than 10 per cent.) occurred at the 6-day count in all tests with moths, with *Stegobium paniceum* (L.), and with *Trogoderma versicolor* (Creutz.). It occurred in film tests only (in which the insects were not fed) with *Oryzaephilus* spp., *Calandra* spp., and with *Tenebrio obscurus* F. A somewhat high control mortality in larvae of *Ptinus tectus* Boield. given food was possibly due to handling.

TABLE II.

Mean responses for the different susceptibility groups.

Group	Mortality % (6 days)	Paralysis % (9 days)	
		Film	Direct spray
Very susceptible	98	100	100
Susceptible	84	100	89
Moderately susceptible ...	56	82	84
Moderately resistant ...	28	80	49
Resistant	9	83	50
Very resistant	1	78	7

Susceptibility to oil.

The types of insects susceptible to R17 oil alone are shown in Table III. The mean 6-day mortalities, found as those in Table II, for the respective groups were 95, 33 and 14 per cent. Most of the larvae listed in Table III were susceptible to direct sprays but not to films. Hewlett (1947*b*) also found *C. granaria* very susceptible to oil, and described the symptoms of oil poisoning in these beetles.

TABLE III.

Types of insects susceptible to R17 oil alone.

Group	Type of insect	
Very susceptible	*S. cerealella*	
	E. cautella	
	E. elutella	
Susceptible	*A. kühniella*	
	C. granaria	
	T. confusum	larvae
	L. oryzae	larvae
Moderately susceptible	*O. surinamensis*	
	O. surinamensis	larvae
	C. oryzae	
	T. castaneum	larvae
	P. tectus	
	S. paniceum	
	T. versicolor	
	G. cornutus	

The other types of insects in Table III showed similar symptoms, but were affected less rapidly than *C. granaria*.

Probably *C. granaria* appears high in Table I because it is susceptible to oil. Although moths were susceptible or very susceptible to oil, early (1-day) counts, done before the oil had taken effect, indicated that they were very susceptible to pyrethrins, with or without piperonyl butoxide. The susceptibility to oil of the moths is not surprising, for mineral oil is effective against another stored-product moth, *Plodia interpunctella* (Hb.), under practical conditions (Cotton, 1956, p. 90).

Relative toxicity of films and direct sprays.

The levels of deposit used were such that the films produced about the same mortalities as the direct sprays for about two-thirds of the types of insects. For most of the remaining one-third the direct sprays produced the higher mortalities, especially of *Alphitobius laevigatus* (F.), *Ptinus tectus* and *Niptus hololeucus* (Fald.). Perhaps the hairs on the beetles of the last two species made them retain relatively large doses when directly sprayed (see Gostick, 1956). Individuals of *Gnathocerus cornutus* (F.) were exceptional, for to them the films were much more toxic than the direct sprays.

Relative toxicity of the pyrethrum formulations.

To each of about three-quarters of the types of insects the P and the P + PB were about equally toxic. The P was conspicuously the more toxic for the following: film—*Gibbium psylloides* (Czenp.), and the larvae of *Tenebrio obscurus*, of *T. molitor* L., of *Ephestia cautella* (Wlk.), and of *Anagasta kühniella* (Zell.); direct spray—*Tribolium castaneum*, *G. psylloides*, and *Tenebrio molitor*, and the larvae of *Tribolium destructor* Uytt. The P + PB was conspicuously the more toxic for the following: film—*C. oryzae* (L.) and *Mezium affine* Boield.; direct spray—*C. oryzae*. Thus, where there was a considerable difference between the toxicities of the P and the P + PB it was more often in favour of the P.

Paralysis.

In experiments with certain of the insects classified as very resistant in Table I, a high proportion remained paralysed on pyrethrum films until the end of the observation period, though few had died; the data for paralysis in Table II indicate this. The adults of *T. destructor*, *T. confusum*, *Gnathocerus cornutus* and the larvae of *Tenebroides mauritanicus* and *Dermestes lardarius* L. were notable in showing a high rate of paralysis but a low mortality when exposed on the films.

The value in practice of insects being paralysed but not killed has never been assessed. Even though there is less than 50 per cent. survival of examples of *Tribolium castaneum* exposed on pyrethrum films for four days, a high proportion of the survivors recover from paralysis if taken from the films (Hewlett, unpublished). *T. destructor* and *E. elutella* can lay viable eggs when paralysed, although, as pointed out by Parkin (1951), beetles normally laying eggs within grains (*e.g.*, *Calandra* spp.) would probably not be able to reproduce if paralysed.

Discussion.

Few general conclusions can be drawn about the relative susceptibility of the different types of insects. Table I indicates that for a given species the larvae were generally more resistant to pyrethrum than the adults. In this Table the group of very susceptible insects contains adults only. Pupae appeared to be at least as resistant as the larvae from which they were derived. Larvae of some species, *e.g.*, *Oryzaephilus surinamensis*, *A. kühniella* and *Tenebrio molitor*, pupated on the pyrethrum films in considerable numbers; some adults emerged from the pupae, but were quickly killed by the films.

If adults only are considered, susceptibility bears a slight relation to systematic position. The moths and the Bruchids were all susceptible or very susceptible to pyrethrins and all the Ptinids at least moderately resistant. The Tenebrionids differed widely in susceptibility, though none were more than moderately susceptible. Among the adults, susceptibility to pyrethrum appeared to be related more closely to the level of normal activity; the greater the activity of the insects when untreated the greater, generally, was their susceptibility. Very active insects tended to be susceptible to oil, liable to high control mortality, or both.

These general conclusions parallel those drawn by Parkin (1953) from his investigation of the toxicity of DDT dust. He found that larvae tended to be more resistant than adults; that, among adults, Bruchids were susceptible, Ptinids resistant, and Tenebrionids variable; and that susceptibility tended to be correlated with activity.

Summary.

With a view to providing information useful in practical control, the relative susceptibility to pyrethrins, and to pyrethrins *plus* piperonyl butoxide, of a series of stored product insects has been determined. Adult moths and beetles of 31 species were investigated, together with the larvae of 16 of these, and that of one other.

The insects were treated with 1·3 per cent. pyrethrins, and 0·3 per cent. pyrethrins plus 3·0 per cent. piperonyl butoxide, in a heavy, highly refined mineral oil (Shell Risella 17). Both formulations were applied in two ways: insects were exposed on sprayed filter papers or were directly sprayed. Insects were also treated with the oil alone by both techniques. While confined on films, and after being sprayed, the insects were kept at 25°C. and 70 per cent. R.H.

Large differences in susceptibility were encountered. The adult moths and Bruchids were susceptible, the adult Ptinids rather resistant, but otherwise susceptibility showed little correlation with systematic classification. The larva of a given species was usually more resistant than the adult. Among the adults of the different species, susceptibility to pyrethrum appeared to be correlated with high activity of the normal insect.

On the whole, 1·3 per cent. pyrethrins and 0·3 per cent. pyrethrins plus 3·0 per cent. piperonyl butoxide were of about equal toxicity.

Acknowledgements.

This work has been carried out as part of the programme of research of the Pest Infestation Laboratory, and the account is published by permission of the Department of Scientific and Industrial Research.

Mr. J. O. Bull and Miss S. Nightingale rendered considerable help by breeding many of the insects used.

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NOTES ON SOME RICE STEM BORERS (LEPIDOPTERA: PYRALIDAE), WITH THE DESCRIPTION OF A NEW SPECIES OF *CHILO* ZINCKEN.

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(Plate VI.)

Much confusion has arisen in the past with regard to the correct application of the names of certain Pyralid rice borers; I hope the following notes and illustrations will clarify the position.

Phycitinae (Anerastiini).

Maliarpha separatella Ragonot (1888:48) (Pl. VI, fig. 1).
Anerastia pallidicosta Hampson (1896:57); **new synonymy.**
Enosima vectiferella Ragonot (1901:391); **new synonymy.**
Maliarpha separatella Ragonot (1901:392).
Ampycodes pallidicosta Hampson (Hampson in Ragonot 1901:393).
Rhinaphe vectiferella Ragonot (Hampson 1918:83).
Rhinaphe pallidicosta Hampson (1918:84).

The genus *Ampycodes* Hampson, 1901, type species *pallidicosta*, falls as a synonym of *Maliarpha* Ragonot, 1888, type species *separatella* (**new synonymy**).

I have examined the type specimens representing the above names. The type of *M. separatella*, from the Cameroons, is in the Zoologisches Museum, Berlin; that of *E. vectiferella*, from Madagascar, is in the Musée d'Histoire Naturelle, Paris. I am indebted to Prof. Dr. E. M. Hering and Monsieur P. Viette for facilities at their respective institutions. The type of *A. pallidicosta* is in the British Museum (Natural History). All the types are males.

Although this species has a similar colour pattern to many other Anerastiini, the form of the uncus and of the gnathos is diagnostic (fig. 1). No variation has been observed in specimens from Africa, China and Burma. Some difficulty exists in the association of female specimens. The figured genitalia (fig. 5) are of a Nyasaland specimen with the same data as a dissected male. Other specimens have a signum consisting of only two plates, others are with only one plate and a bred female recently received from Senegal associated with a male is without a signum. I provisionally treat this as merely individual variation; further bred material is necessary before this point can be safely decided.

Specimens from Ghana, Cameroons, Nyasaland, Madagascar, Burma and China are in the British Museum (Natural History). Specimens from Ghana, Senegal and Swaziland have been bred from rice.

Schoenobiinae.

Schoenobius incertulas (Walker) (Pl. VI, figs. 2 & 3, text figs. 3 & 7).
Chilo incertulas Walker (1863*a*:143).
Catagela? admotella Walker (1863*a*:192).
Schoenobius punctellus Zeller (1863:4).
Schoenobius minutellus Zeller (1863:5).
Tipanaea bipunctifera Walker (1863*b*:523).
Chilo gratiosellus Walker (1864:967).
Apurima gratiosella Butler (1880:690).

Figs. 1–8.—Male genitalia:
1. *Maliarpha separatella* Rag. 2. *Chilo phaeosema*, sp. n.
3. *Schoenobius incertulas* (Wlk.). 4. *Scirpophaga chrysorrhoa* Zell.
a = aedoeagus, b = right valve, c = anellus.

Female genitalia:
5. *Maliarpha* sp. ? *separatella* Rag. 6. *Chilo phaeosema*, sp. n.
7. *Schoenobius incertulas* (Wlk.). 8. *Scirpophaga chrysorrhoa* Zell.
Approximate magnifications: ♂♂, × 16; ♀♀, × 10·5.

This species has usually been recorded in the economic literature as *S. bipunctifer* (Walker) or *S. incertellus* (Walker) (Jepson, 1954).

The species is sexually dimorphic; the forewings in the male are brownish-ochreous with darker markings; in the female whitish-yellow to yellowish-orange with a single fuscous discal spot. The sexes have often been recorded as different species, and were so given in the last monograph of the subfamily (Hampson, 1895: 915–6).

Also under *Schoenobius*, Hampson (1895: 916) lists *S. adjurellus* (Walker), with *S. brunnescens* Moore and *S. celidias* Meyrick as synonyms. These names are based on male specimens which have a similar wing-pattern to, and have been confused with, the male of *S. incertulas*. Although *S. adjurellus* is a related species of *Schoenobius*, the species represented by the names *S. brunnescens* and *S. celidias* is quite distinct and is correctly placed in *Scirpophaga*. No female specimens have previously been associated with these male *Scirpophaga*. Investigation of that genus, however, reveals a species with a similar distribution represented only by female specimens: *Scirpophaga chrysorrhoa* Zeller, a species with unicolorous white wings. I have no doubt that these males and females should be associated as one species and propose the following synonymy:

Scirpophaga chrysorrhoa Zeller (Pl. VI, figs. 5 & 6; text figs. 4 & 8).

Scirpophaga chrysorrhoa Zeller (1863: 1).
Schoenobius brunnescens Moore (1888: 225); **new synonymy.**
Schoenobius celidias Meyrick (1894: 475); **new synonymy.**

Distribution: India, East Pakistan, Ceylon, Andaman Is., Thailand, Borneo, southern China, Northern Australia. This species has not yet been recorded as a rice borer. Possible confusion with *S. incertulas* should not, however, be overlooked.

CRAMBINAE.

Chilo phaeosema, sp.n. (Pl. VI, fig. 4).

♂ 20 mm., ♀ 27 mm. Labial palpi about twice length of head, ochreous, suffused with fuscous distally. Forewing ochreous with a prominent black discal dot; a dark band formed by black scales interspersed with those of the ground colour, from apex to below discal dot, with another forming a bar across the cell basad of the discal dot and a continuation below Cu_1 at one-third parallel to apical band. These two dark bands form an incomplete ring round the discal dot, somewhat like a spectacle frame. A brown subterminal line is present from the apical black band to near tornus, curving away from outer margin towards tornus and towards apex; terminal line represented by a row of black dots on the veins; cilia pale brownish with a lighter medial line. In the male, costal area of forewing suffused brownish. Hind wing whitish, in male suffused with fuscous with an imperfectly developed black terminal line fading to fuscous towards tornus and apex. Colour of cilia that of the ground colour, with a darker medial line. Underside: Brownish-ochreous in male, the greater part of the forewing, with the exception of the costal and terminal areas, strongly suffused fuscous; veins crossing the terminal area fuscous; hind wing weakly suffused fuscous; terminal dots and cilia in both wings as upperside. Forewings of female whitish-ochreous, hind wings whitish, terminal dots and cilia of both wings as upperside.

Genitalia as figured (figs. 2 & 6), note the absence of the costal lobe present in the male of *C. zonellus*.

The species is somewhat similar to *C. zonellus*, the darker markings in that species, however, are more extensive, and the ground colour of African specimens generally very much darker, especially in the male.

Type material: Holotype ♂; Makaholi, Southern Rhodesia, 15.iv.1955 (*D. J. W. Rose*); rice borer. Allotype ♀: data as holotype, 14.iv.1955.

Distribution: Tanganyika, Nyasaland, Southern Rhodesia.

Specimens of this species in the British Museum (Natural History) were identified by Hampson as *Diatraea africana* Aurivillius (1910: 54), although they do not agree well with the original description and figure. Through the kindness of Dr. R. Malaise of the Naturhistoriska Riksmuseum, Stockholm, I have been able to examine the type specimens of *D. africana*. They are identical with *Parerupa diagonalis* Hampson (1919: 539). In the original description of *P. diagonalis*, Hampson lists a specimen collected by Sjöstedt from Meru. Aurivillius described *D. africana* from six female specimens; I select one of these, bearing the label "Meru Nieder, Sjöstedt 1905, 24 Nov" and with the determination label in Aurivillius' handwriting, as the lectotype.

D. africana should be transferred to the genus *Parerupa* Hampson (**new combination**); *P. diagonalis* falls as a synonym of *P. africana* (**new synonymy**).

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FIG. 1. *Maliarpha separatella* Rag., ♂.

FIG. 4. *Chilo phaeosema* n.sp., holotype .

FIG. 2. *Schoenobius incertulas* Walk., ♂.

FIG. 5. *Scirpophaga chrysorrhoa* Zell., ♂.

FIG. 3. *S. incertulas* Walk., ♀.

FIG. 6. *S. chrysorrhoa* Zell., holotype .

(Approximately twice natural size.)

THE YIELD OF *LASIODERMA SERRICORNE* (F.) (COL., ANOBIIDAE) FROM A GIVEN QUANTITY OF FOODSTUFF.

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Although pests of stored products are reared in a number of laboratories as experimental animals, the maximum yield or crop of a species that can be reared on a given quantity of foodstuff has apparently not been determined. A related question which has not been quite so neglected is what quantity of foodstuff is used per individual of a species in the course of its development, when there is an ample supply (Fraenkel & Blewett, 1944; Gunn & Knight, 1945; Richards, 1947) or when there is barely enough for complete development (Gunn & Knight, 1945). Information of either sort has a physiological interest when comparisons can be made between species, between foodstuffs, or under different physical conditions. Information on maximum yield should throw light also on the economy of populations living on residues of produce in the fabric of storage buildings.

Another allied question is that of finding the optimum yield of insects which can be removed from a population growing on a food supply which is self-regenerating or which is periodically renewed. This is a problem of fisheries and wildlife management, but it has also been studied experimentally by means of cultures of *Tribolium* (Watt, 1955).

The species selected for the present experiments was the Cigarette Beetle, *Lasioderma serricorne* (F.), a pest of tobacco and stored foodstuffs. This species has the following desirable features: it has a fairly short life-cycle (7 weeks on wheatfeed at 25°C. and 70 per cent. relative humidity); it develops well on a convenient food material; the adult does not feed; the eggs are laid loosely in the food, from which they can easily be separated. Its physical ecology has been studied by Howe (1957) and others. Wheatfeed is a type of millers' offal widely used as an animal feeding-stuff and comprises, chiefly, bran and endosperm in somewhat variable proportions.

The first author carried out the experiments; the second author initiated the work and prepared the present account; Mr. R. W. Howe contributed the statistical analysis. The paper is published by permission of the Department of Scientific and Industrial Research.

Observations on Cultures in the Insectary.

In the insectary, cultures of *Lasioderma* are set up by adding 200 adults to roughly 200 g. of wheatfeed at 25°C. and 70 per cent. relative humidity. Formerly, 5 per cent. of dried yeast was added, but this appears to be unnecessary (Howe, 1957).

In one such culture, the adult progeny of about 100 females was counted, and found to be about 80 per female, or 40 per g. of foodstuff. The latter figure is not specially significant since the food material was by no means exhausted.

In an older culture, which had been left for about 30 weeks, the contents appeared to consist of dead adults, cast skins, and faecal matter. On closer examination, two live adults and four live larvae were found. The dead beetles

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amounted to about 21,000, *i.e.*, probably somewhat more than 100 per g. of foodstuff put into the culture. If, as in the first culture mentioned, the first filial generation was about 8,000, the later generations between them produced only 13,000.

Methods.

The experiments were conducted in a controlled room at $25 \pm 0{\cdot}5$°C. and 70 ± 2 per cent. relative humidity. The wheatfeed used in the experiments was heat-sterilised for four hours at 60°C., then spread out in a wide dish and exposed for a week to the experimental conditions, and finally stored in a sealed jar in readiness for use. Aliquots of the food material were put into flat-bottomed glass specimen tubes, one inch wide and 2 inches high ($2{\cdot}5 \times 5$ cm.), each closed by fine cotton cloth held in place by a cork with a central hole.

Eggs were collected by placing a large number of the beetles on wheatfeed which had been passed through a sieve of 72 meshes per inch (28 per cm.); after 24 hours the wheatfeed was passed through a coarse sieve to remove the beetles, and finally through one of 60 meshes per inch (24 per cm.), which retained the eggs. The eggs were sorted into batches, normally of 100 each, under a dissecting microscope, and one batch added to each tube. The tubes were placed in individual shallow dishes on a tray containing oil.

When, in due course, adults began to appear, these were removed daily from the tubes, counted and weighed, and discarded.

The results of a preliminary experiment having shown the numbers of *Lasioderma* which could be reared on 1 g. of the foodstuff, the principal experiment was so designed as to leave some of the tubes of wheatfeed incompletely exploited in the first instance, so that the numbers of insects required to complete the process could be approximately calculated and added later. It was planned that in this way some of the tubes of foodstuff should escape any marked over-exploitation and possible reduction in yield from this cause.

In a subsidiary experiment (p. 197), the food supply was more severely over-taxed than in any part of the principal experiment, and in another (p. 198) it was less severely exploited.

The results of the principal experiment were treated statistically by Mr. R. W. Howe, using analysis of variance. The significance (5 per cent. level) of the differences arising from the use of four different quantities of foodstuff in the principal experiment was tested by the range method.

The Principal Experiment.

Stage 1.

The experiment was set up as follows:—

A. Six tubes each with 1·000 g. wheatfeed and 100 eggs
B. ,, ,, ,, ,, 0·875 g. ,, ,, ,, ,,
C. ,, ,, ,, ,, 0·750 g. ,, ,, ,, ,,
D. ,, ,, ,, ,, 0·625 g. ,, ,, ,, ,,
E. One control tube with 1·000 g. wheatfeed and no eggs.

The results are shown in Table I (entries for stage 1). Each group of six replicates is entered as a single unit. The following conclusions may be drawn:—

1. The smallest quantity of food supplied (D) was too little; there was only 61 per cent. survival to the adult stage in D compared with about 90 per cent. in A, B and C (the differences between these three are not significant).
2. Taking biomass of adults (total wet weight) as the criterion, the food supply in D was again shown to be inadequate; furthermore, although the differences between C and B and between B and A are on the borderline of statistical

significance, they form an ascending series which probably represents a real increase in yield with the increments in the food provided.

3. Considering mean individual weights, these fell off by significant steps as crowding increased or the food supply decreased (A→B→C→D).
4. The interim yield of adults per g. of food, whether measured as numbers or as biomass, increased significantly from A to C, with the increase in the initial density of eggs; but in D, where the food supply was over-taxed, it was significantly lower than in C.

TABLE I.

Yield of adult *Lasioderma* from four different amounts of wheatfeed, exploited by two successive populations. For further explanation, see text. Each group of six replicates is entered as a unit.

	Stage	Treatment			
		A	B	C	D
Weight of food material (g.) :—	—	6·00	5·25	4·50	3·75
No. eggs added	1	600	600	600	600
	2	365	205	133	0
	1 + 2	965	805	733	600
Total adults emerged	1	535	545	557	366
	2	112	76	21	—
	1 + 2	647	621	578	366
% survival to adult	1	89·2	90·8	92·8	61·0
	2	30·7	37·1	15·8	—
	1 + 2	67·1	77·1	78·9	61·0
Biomass of adults *i.e.*, total wet wt. (mg.)	1	1073	991	928	519
	2	203	139	32	—
	1 + 2	1276	1130	960	519
Mean indiv. weight (mg.)	1	2·01	1·82	1·67	1·42
	2	1·81	1·83	1·52	—
	1 + 2	1·97	1·82	1·66	1·42
No. eggs added per g. food	1	100	114	133	160
	1 + 2	161	153	163	160
No. adults per g. food	1	89·2	103·8	123·8	97·6
	1 + 2	107·8	118·3	129·1	97·6
Biomass of adults (mg.) per g. food	1	179	189	206	139
	1 + 2	213	215	213	139
Wt. of remaining material (g.)	—	3·164	2·815	2·217	1·836
% foodstuff metabolised	—	47·3	46·3	50·7	51·0
Yield of insects (g.) per g. foodstuff metabolised	—	0·45	0·46	0·42	0·27
Developmental period (weeks)	1	6·5–9	6·5–9·5	7–10	7–27
	2	8–14	8–17	15–18	—

Stage 2.

We have seen that while the food supply in D was inadequate, the supply in C was enough to ensure the maximal developmental survival (though not maximal biomass of adults). For the purposes of the second stage of the experiment, the hypothesis was adopted that 3·900 g. (6 × 0·650) would be just enough food for maximal survival from 600 eggs to the adult phase. On this basis, 4·500 g. (6 × 0·750) should support 6 × 115 insects, 5·250 g. (6 × 0·875) should support 6 × 135, and 6·000 g. (6 × 1·000) should support 6 × 154. It was intended that eggs should be added to the original tubes of foodstuff so that for each tube the number of eggs added *plus* the number of adults already emerged would be equal to these calculated numbers. This was done in the case of group C, but in B somewhat fewer than the calculated number of eggs was added (total 205 added in stage 2 instead of 265), and similarly in A a total of 365 eggs was added in stage 2 instead of the calculated 389. If these differences had been of any significance, the chief effect to be expected was that B should have been somewhat less heavily exploited than C or A, in stage 2 of the experiment. If any such tendency existed, its effect, as judged by the differences between the results for B and A, was very slight (*e.g.*, in mean individual weight, and in no. adults per g. food). The much more marked differences between the results for A and C cannot be attributed to the small discrepancy between the calculated 389 and the actual number (365) of eggs added to A in stage 2.

As before, when the adults appeared, they were removed daily, weighed and discarded. The results are shown in Table I (entries for stage 2).

Stage 3.

To find whether the foodstuff was quite exhausted, five more eggs were added to each tube. The larvae all died at an early stage of growth. It does not follow that the value adopted for the hypothesis of stage 2, or the numbers of eggs added, were therefore exactly correct. As we shall see, rather too many eggs were in fact added to the tubes of sets A, B and C in stage 2.

The conclusions to be drawn from the whole experiment, involving the complete exploitation of each supply of food, are as follows:—

1. *Percentage survival to adult stage*:—The relatively low value of A (in stages 1 + 2) was a result of the events of stage 2. Evidently the hypothesis used in stage 2 was not quite correct, so that, judged by percentage survival of the eggs added in stage 2, too many eggs were added in B, a greater surplus in A, and the greatest surplus (proportionately to the capacity of the food material to support their development to the adult stage) in C; but in C, the absolute numbers involved in stage 2 were small, which reduced their influence on the final figure.

2. *Mean individual weight*:—Here the values were determined chiefly by stage 1, and simply reflect the decreasing food supply per 600 eggs in the series A→B→C→D. Even in A, stage 1, the beetles were distinctly undersized (*cf.* p. 198).

3. *Biomass of adults*:—As in stage 1, the total yields of adults reflect the differences in the amounts of food supplied. This relationship is viewed more precisely below (4).

4. *Biomass of adults per g. of food*:—Except in D, where the yield was reduced by the over-taxing of the food supply, *the yield of adults per g. of food is constant at about 214 mg.*

5. *Number of adults per g. of food*:—There was a significant falling-off in D (as compared with C or B) caused by overcrowding, or over-taxing of the food supply, but a significant increase from A to C. Since the mean individual weights decreased from A to C, while the number of adults from each g. of food increased, the effect of reducing the food supply per individual egg was to yield more and smaller adults per g. of food (thus maintaining the constant biomass yield noted

in 4). In D, with a more extreme food shortage, not only were the beetles still smaller, but also there were fewer of them per g. of food.

6. *Percentage foodstuff metabolised*:—The weight of material metabolised, *i.e.*, broken down into non-solids and/or incorporated into the insects, is taken to be the difference between the initial weight of foodstuff and the weight of material remaining at the end of the experiment. (The remains are chiefly faecal matter that would have passed through the insects at least once, but also some cast skins. Strictly, the latter should be excluded from the category of non-utilised material, but they were mostly broken down into small pieces, difficult to separate from the other material, and the error involved is not great.) The proportion of material metabolised is 46 or 47 per cent. in A and B (the difference is not significant) and about 51 per cent. in C and D. It is not clear why the exploitation of the material should have been more complete in C than in B; the final overall yields in biomass per g. or in numbers of adults per g. in these two were not significantly different, nor were the numbers of eggs applied per g. of the food; but in stage 1 all three were significantly greater in C than in B, and it may be that severe exploitation by a first infestation is more efficient than a less severe one supplemented by a second infestation, for in the latter case the young larvae may suffer gravely from the poor quality of the remaining food material.

7. *Yield of insects (g.) per g. of food metabolised*:—This is an index of physiological efficiency, its value depending on the state of the food material and the condition of the insects. The values for A and B are closely similar (0·45 and 0·46), whereas that for C is a little lower (0·42). It is difficult to decide whether the value for C is depressed as a result of the over-taxing of the food supply in stage 1: more eggs were added per g. of food and, although the percentage survival to the adult stage was not significantly lower than in B and A, the adults were individually lighter; moreover, the proportion of the foodstuff metabolised was about 51 per cent., as in D, not about 47 per cent., as in B and A. On the whole it seems best to adopt a maximal yield figure of 0·46, based on A and B, and to consider the value for C as being slightly depressed by over-exploitation of the food supply.

In C and D, the combination of reduced yield per g. metabolised with a raised percentage of foodstuff metabolised is open to various interpretations. Possibly in the absence of adequate food the insects metabolised more low-grade material which gave little basis for growth. Possibly also, with the smaller ratios of food to insects, more energy was expended in competition.

8. *Developmental period*:—In stage 1, the developmental period varied between the same limits, approximately, in A, B and C, but some individuals in D developed very slowly, presumably because of the over-taxing of the food supply. In stage 2, the generally retarded development in A and B can be similarly interpreted, while the more marked retardation in C reflects the fact that the nutritive value of the medium was almost exhausted from an early stage.

Subsidiary Experiments.

In one of these experiments, 100 eggs were added to each 0·50 g. of food (6 replicates), so that the food supply was more severely over-taxed than in any part of the principal experiment. Under these more severe conditions, only 60 mg. weight of adults was produced per g. of foodstuff. As well as starvation, cannibalism may also have played some part in reducing the yield to this low level, for on several occasions larvae were observed eating pupae in cocoons.

Development was considerably retarded: the main emergence of adults was from 9 to 19 weeks from the start of the experiment. Although some larvae remained in each tube, no more adults emerged between the 19th and 29th weeks. At the end of this period all but one of the larvae in each tube were transferred to separate tubes with excess food. Most of the larvae transferred to fresh food

became adult within about a month, but those left in the original tubes of used material were still in the larval stage two months later; after yet another month they had all died, presumably by starvation. The weights of the adults emerging from the retarded larvae that had been transferred to tubes with excess food were much higher (mean 2·3 mg.) than the weights of those which had emerged from the original experimental tubes (mean 1·3 mg.).

In another experiment, in which only 60 eggs were added to each 1 g. of food (6 replicates), the mean weight of the adults produced was 2·4 mg. This is appreciably higher than the mean weights of beetles in the principal experiment, but is quite close to the mean weight of 2·6 mg. for adults bred in isolation (otherwise as in these experiments; R. W. Howe, unpublished data). Hence body weight is evidently not reduced by any substantial "group effect" such as that found in *Ptinus tectus* Boield. at relatively low densities by Gunn & Knight (1945).

Discussion.

The primary aim of the experiments was to determine the maximum yield of adult *Lasioderma* per g. of wheatfeed at 25°C. and 70 per cent. relative humidity. This was found to be 0·214 g. (A, B and C). Correspondingly, the weight of foodstuff was reduced to about one-half, the other half representing material broken down into free water or carbon dioxide, or incorporated into the bodies of adult insects. If we say that 0·48 of each 1 g. of food was metabolised in these ways (mean of A, B and C), and 0·21 g. of this was transformed into adult insects (the weight of the eggs added being negligible), the other 0·27 g. of it represents the material dissipated as CO_2 and water. In short, nearly 50 per cent. of the food material was metabolised, nearly 44 per cent. of this (21 per cent. of the whole) being converted into insect material. This figure of 21 per cent. may be compared with those of 25 per cent. for the pig (on high-quality feed) and 20 per cent. for the growing cockerel, quoted by Trager (1953).

The values for *Lasioderma* would no doubt vary with the physical conditions and more particularly with the composition of the food material. Although wheatfeed is a variable and ill-defined product, the figures serve to show approximately the yield of this insect from this type of foodstuff, and more precisely the relative efficiency of different ways of exploiting the same food supply.

One of the entries in Table I shows the yield of insects (g.) per g. of foodstuff metabolised (*i.e.*, per g. loss of weight of the material). This ratio may also be calculated from the results of Fraenkel & Blewett (1944), who bred three species of stored-products pests at 25°C. and 70 per cent. relative humidity. The figures are as follows:—

Dermestes maculatus Deg. on brewers' yeast + fructose + 1 per cent. cholesterol: 0·39.
Tribolium confusum Duv. on patent flour + 5 per cent. yeast: 0·40.
Ephestia kuehniella Zell. on wholemeal flour: 0·43.

These may be compared with the present results for *Lasioderma serricorne* on wheatfeed: 0·46.

In all cases the calculations are based on the weight of food and insects at 70 per cent. relative humidity, not the dry weight. Whereas we weighed the young adults, Fraenkel & Blewett weighed pupae. In view of the variety of species and food materials, it is interesting that these results are so similar. Richards (1947, p. 20) determined the loss in dry weight of wheat grains on which *Calandra granaria* (L.) had been reared. For each weevil produced (mean weight 2·41 mg.) the dry weight loss was 13·8 mg. For the present comparison, this dry weight loss must be converted to the corresponding figure for grain at 70 per cent. relative humidity, assuming a corresponding moisture content of 14 per cent. on a wet weight basis: the converted figure is 16·04 mg. The corresponding value for

g. insect produced per g. of foodstuff metabolised is 0·15, *i.e.*, only one-third of the value for *Lasioderma* and slightly more than one-third of the values for the other species. Whether the cause of this difference lies in the dietetic inferiority of wheat endosperm (without added yeast), or in some peculiarity of *C. granaria*, or whether the agreement between the other four species is not typical of stored-products pests in general, must remain unsettled for the present.

From our results it appears that the most efficient way of exploiting a supply of food, to achieve the maximum yield in weight of adult insects per gramme of material, is to add just the right number of eggs at the start. If too many are added, as in D, starvation, and probably other density effects, reduce the yield (*cf.* the experiments of Ullyett (1950) and Nicholson (1954) on blowflies). If too few eggs are added, the yield is naturally reduced; and if an attempt is made to utilise the remaining food material by adding a second " generation " of eggs to a food supply which is largely used up, the combined yield never reaches the maximum level, probably because the effects of the vitiated or impoverished food material are particularly harmful to the young larvae.

Summary.

An experiment was designed to ascertain the maximum yield of adults of the Cigarette Beetle, *Lasioderma serricorne* (F.) that could be reared from a given quantity of foodstuff. Equal numbers of eggs of this species were added to batches of tubes containing different weights of wheatfeed, and the resulting adults were removed, counted and weighed.

The weights of wheatfeed had been chosen so that in some of the batches of tubes it would not be completely exploited. When emergence of adults was complete, further numbers of eggs, which were calculated to produce approximately the number of larvae necessary to complete the process in each batch of tubes, were then added, and the resulting adults again removed, counted and weighed.

The maximum biomass (wet weight) of adults of *L. serricorne* which could be reared from egg to adult per gramme of wheatfeed at 25°C. and 70 per cent. relative humidity was found to be 0·214 g. (108 to 129 specimens, all more or less undersized, and many with a retarded rate of development, compared with insects given ample food). In addition to the 21 per cent. of the food converted into adult insects, another 27 per cent. by weight of the original foodstuff was lost, presumably as water and carbon dioxide, leaving just over 50 per cent. undigested residue, most of which was faecal matter that would have passed through the insects at least once.

The yield of insects per g. loss of weight of the foodstuff was 0·46 g. (wet weights), which is very close to the corresponding figures calculated from the results of Fraenkel & Blewett for *Dermestes maculatus* Deg., *Tribolium confusum* Duv. and *Ephestia kuehniella* Zell. on various foods, but three times as great as the corresponding figure calculated from Richards' results for *Calandra granaria* (L.) in wheat.

There was evidence suggesting that a truly maximal yield (slightly greater than in these experiments) might be attained by adding an optimal number of eggs to the food at the start, instead of adding a second population to an incompletely exploited food supply.

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A PRELIMINARY SURVEY OF THE DISTRIBUTION AND HOST-SPECIFICITY OF TICKS (IXODOIDEA) IN THE BECHUANALAND PROTECTORATE.*

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Between December 1954 and July 1956, the author, assisted by Mr. W. Brauns of the South African Institute for Medical Research, was able to undertake several trips to the Bechuanaland Protectorate (see map 1), in order to study the arthropod and helminth parasites of man as well as of wild and domestic animals. These trips were made possible by Dr. M. L. Freedman, former Director of Medical Services of the Bechuanaland Protectorate, and were financed by the Administration of the Protectorate, the South African Council for Scientific and Industrial Research, Pretoria, and the South African Institute for Medical Research, Johannesburg. During the course of the survey, much valuable help was received from the Veterinary Department of the Protectorate.

This paper deals with the ticks collected by Mr. Brauns and the author, and also those collected by Mr. D. H. S. Davis of the Plague Research Laboratories of the Union Health Department, during a trip to the Protectorate in 1946.

The data at present available on the distribution and host-specificity of ticks in the Bechuanaland Protectorate are still very incomplete, and the collections discussed below do not represent more than a preliminary contribution from which general conclusions can only be drawn with the greatest caution. A great deal more collecting will have to be done before it will be possible to give a reliable account of the distribution and economic significance of the most important species of ticks.

Ixodes pilosus Koch—Sourveld Tick.

Records.

Machaneng Mines nr. Kanye, 17.xii.56—dog—2 ♂♂, 5 ♀♀.

Distribution.

This is the first time that *I. pilosus* has been found in the Bechuanaland Protectorate. In the Union, *I. pilosus* occurs " in grass veld and not in scrub or Karroo veld. Its distribution in grass veld is, however, very regional and patchy and is mainly confined to the coastal areas and to parts of the Northern Transvaal. A careful study of the data available shows it to be present only in areas having what is known locally, in each instance, as ' sour veld '. Sour veld is a general term covering long rank grass, growing in more or less larger tufts in areas of a relatively high rainfall; it is usually perennial, and unpalatable to stock when mature or dry; the soil is usually poor." (Theiler, 1950*b*).

No exact data are available about the ecological requirements of the tick. How much the rainfall affects its distribution is difficult to assess. *I. pilosus* is normally absent from the drier parts in southern Africa, and its finding in the Bechuanaland Protectorate is unexpected and certainly an isolated occurrence. Theiler says that the influence of precipitation appears to be indirect rather than

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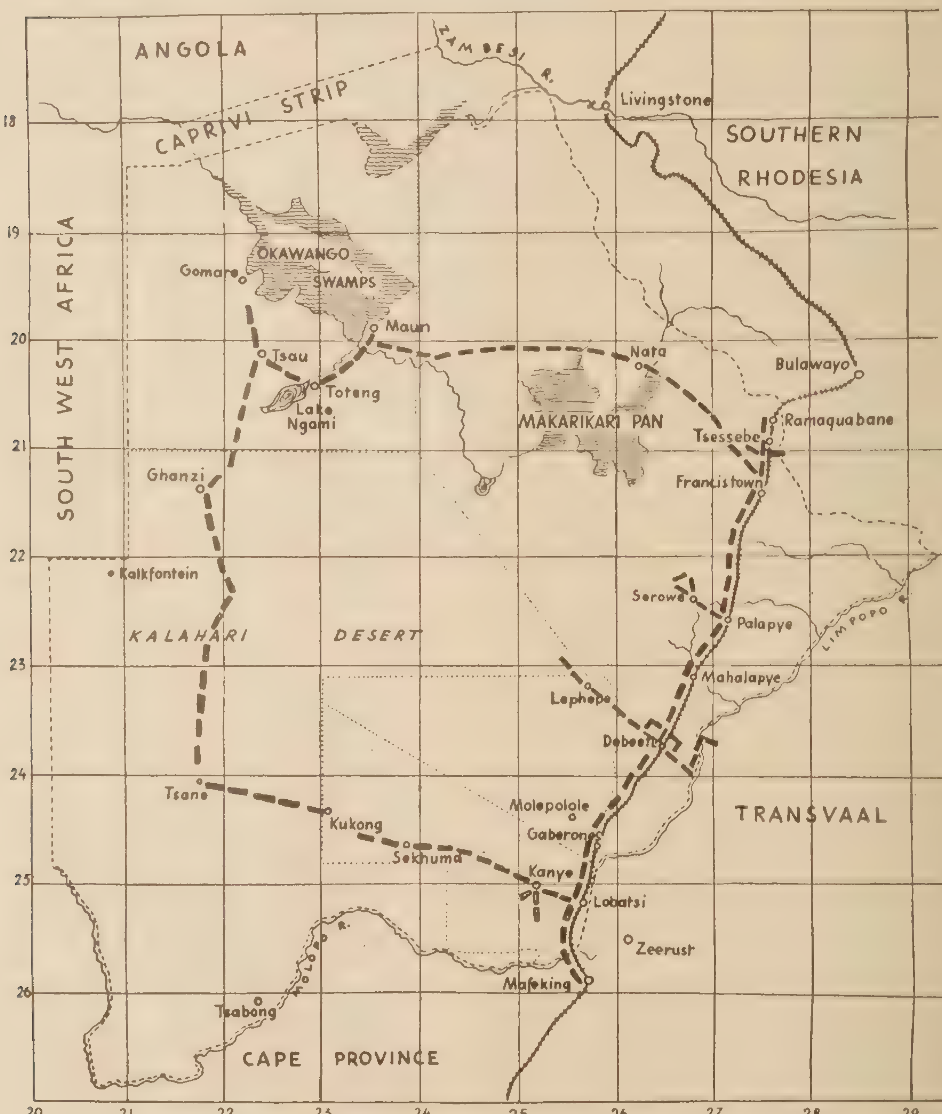
direct, and that the vegetation suitable for this tick varies with the rainfall. The length of the grass is probably most important, and Theiler is "tempted to assume that the rougher and higher the sourveld the greater the chances of survival of the tick".

In the Kanye district, there are some places with a grass vegetation similar to the sourveld, but this formation is rather patchy. The question is whether *I. pilosus* is a real indigenous species in this district, or whether it has been imported with dogs or other domestic animals from other places, for instance from the northern Transvaal.



Map 1.—Itinerary.

The distribution of *I. pilosus* in the Union has been mapped by Theiler (1950*b*). The records from E. Africa, Nyasaland and S. Rhodesia mentioned by former authors have to be re-checked because this species has often been confused with other species. The genus *Ixodes* is a difficult taxonomic unit which is being reviewed by Dr. D. R. Arthur.

Host-specificity.

I. pilosus is a three-host tick and has often been found on the dog, but it occurs mainly on buck (bushbuck, oribi, steinbok, reedbuck, etc.) and has also been taken from the buffalo and the lion. Some of the farmers in the Union blame the kudu and the bushbuck for maintaining the tick in the veld. In Bechuanaland a great number of antelopes, including the kudu, have been carefully examined for ticks, but *I. pilosus* has never been found to infest them.

Economic importance.

I. pilosus has been erroneously accused of causing paralysis in sheep (*I. rubicundus* Neumann is the true Karroo paralysis tick). It is not known to transmit any disease to man or domestic animals.

Amblyomma hebraeum Koch—The South African Bont Tick.

*Records.** (See map 2.)

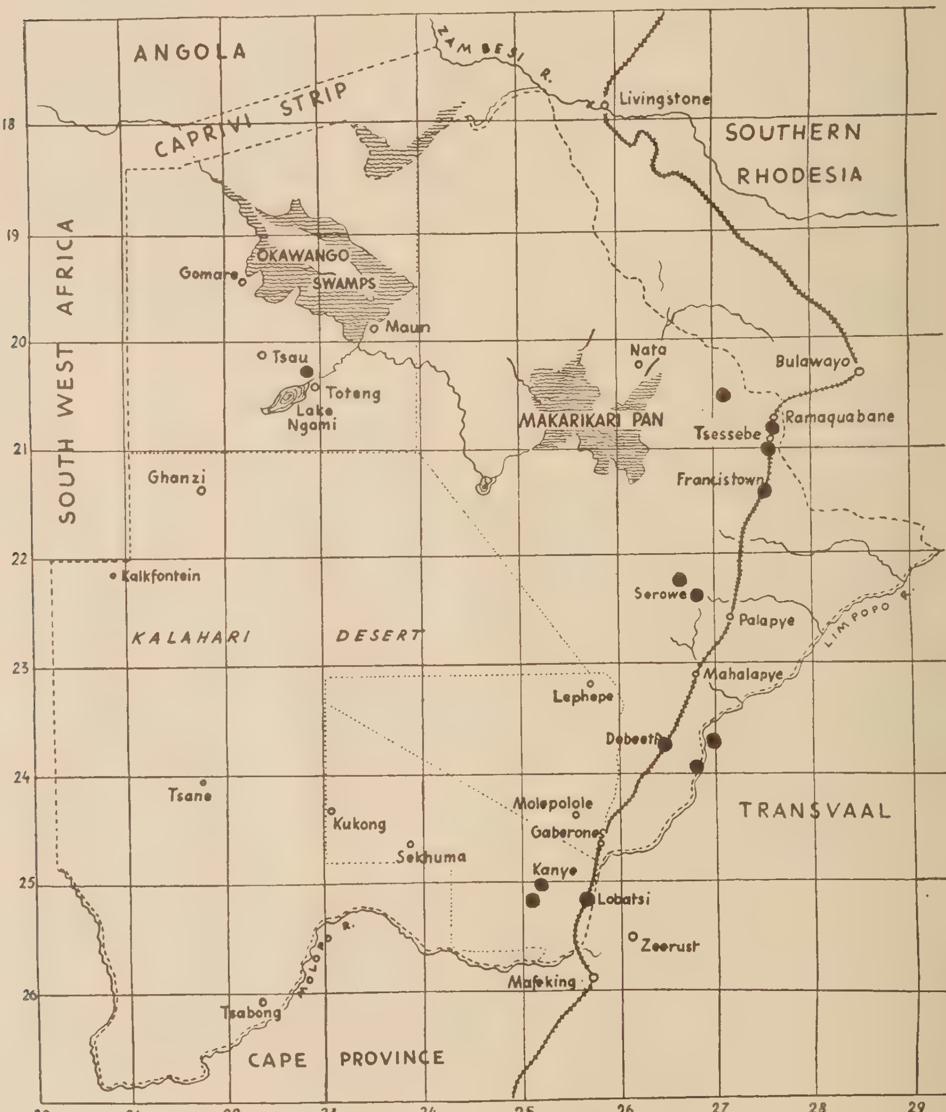
LOBATSI (abattoir), 31.i.56 and 22.ii.56—cattle, many of them heavily infested with adult ticks. The animals are brought to the abattoir from various parts of the country; the exact original localities cannot be stated: KANYE, 16.xii.55 goat—1♂, 1 N.; 22.i.56—*Papio comatus*, Chacma Baboon—1 L.; 15.xii.55 *Pterocles burchelli*, Spotted Sand-grouse—3 L.; 16.xii.55—*Pternistis swainsoni*, Swainson's Francolin—1 N.; 16.xii.55—*Plocepasser mahali*, White-browed Sparrow-weaver—1 L.; 22.i.56—*Turdoides leucopygia*, White-rumped Babbler—13 L.: SEKHWAWA,† 8.x.55—cattle—heavily infested: DEBEETE (quarantine camp), 20.i.56—cattle—moderately infested with adult ticks; (25 m. SE), 23.vii.56—*Aepyceros melampus*, Impala—1 N., 11 L.; (25 m. SE), 28.vii.56—*Sylvicapra grimmia*, Grey Duiker—7 N.; (25 m. SE), 20.vii.56—*Raphicerus campestris*, Steinbok—2 N.; (25 m. SE), 20.i.56—*Vulpes chama*, Chama Fox 2 N., many larvae; (quarantine camp), 22.vii.56—*Lepus saxatilis*, Scrub Hare 1 N., many larvae; (45 m. E), 19.vii.56—*Cercopithecus aethiops*, Vervet Monkey —1 L.; (20 m. SE), 15.vii.56—*Francolinus sephaena*, Crested Francolin—4 N., many larvae; (20 m. SE), 15.vii.56—*Pternistis swainsoni*, Swainson's Francolin 3 L.; (quarantine camp), 19.xii.55—*Thripias namaquus*, Bearded Woodpecker-1 N.; (quarantine camp), 19.xii.55—*Lophoceros flavirostris*, Yellow-billed Hornbill—many L.; (quarantine camp), 19.xii.55—*Erythropygia paena*, Robin Warbler—1 L.; (quarantine camp), 19.xii.55—*Coracias garrulus*, European Roller 1 L.: SEROWE, 14.i.56—*Pternistis swainsoni*, Swainson's Francolin—4 N., many larvae; THABALA nr. SEROWE, 16.i.56—cattle and horses—heavily infested with adults and nymphs: FRANCISTOWN (abattoir), 7.ii.56—cattle—moderately infested with adults and nymphs; 18.xii.54—*Lophoceros erythrorhynchus*, Red-billed Hornbill—1 N. (Dias, 1955*c*); 18.xii.54—*Centropus senegalensis*, Fleck's Coucal—2 N., 1 L. (Dias, 1955*c*): BOSOLI ‡ TSESSEBE, 9.i.56 and 1.xi.56—cattle—13 ♂♂, 8 ♀♀ (this is only a slight infestation compared with the number of other ticks found on the animals); 23.xii.55—dog—2 N.; 3.i.56—*Sylvicapra grimmia*, Grey

* It is of the greatest importance to note very carefully whether the hosts were found infested with adults (♂ ♀) or with immature stages (L, N), or with both, because the immature stages of certain tick species, especially of the genus *Hyalomma*, live on hosts which are different from, and usually smaller than, those infested by the adults.

† South-west of Kanye.

‡ Between Francistown and TSESSEBE.

Duiker—1 N., many larvae: Nr. SEBINA,† 19.xii.54—*Numida mitrata*, Crowned Guinea-fowl—7 L. (Dias, 1955*c*): Nr. TOTENG (Lake Ngami), 4.i.55—*Lophoceros erythrorhynchus*, Red-billed Hornbill—1 N. (Dias, 1955*c*).



Map 2.—● = *Amblyomma hebraeum* Koch.

Distribution.

A. hebraeum is widely distributed in the Union and inhabits all three types of the South African parkland as well as the forest zones westwards to the district of Mossel Bay. It is absent from the desert shrub areas, the evergreen sclero-

† West of Tsessebe.

phyllous bush of the Western Province and most parts of the grass lands of the high- and middleveld (see Theiler, 1948). It is said to exist in Southern Rhodesia as an introduced tick; in Mozambique it is a common and indigenous species south of the Save river (Dias, 1951).

These findings agree very well with those in the Protectorate, where *A. hebraeum* was found in the parkland vegetation of the east and near Lake Ngami. It was not detected in the dry area of the Kalahari, where one would not expect it according to its known humidity preference.

Host-specificity.

A. hebraeum is a three-host tick and infests a wide range of wild and domestic animals. It is one of the most important cattle-ticks in southern Africa and, like the closely related Tropical Bont Tick, *A. variegatum* (F.), feeds in all stages on cattle and other domestic and wild ruminants. Smaller mammals and birds belonging to various unrelated groups are very often infested with the immature stages. This is apparent also in the collections from the Protectorate.

Economic importance.

A. hebraeum has been found infected with the causal agent of tick-bite fever (*Rickettsia conori*), a human disease which is contracted by almost every European newcomer to the Protectorate. It is also a transmitter of heartwater (*Cowdria ruminantium*) in cattle, sheep and goats, this disease also being widespread in the Protectorate. Another transmitter of heartwater is *A. variegatum*, which is known to occur in the Caprivi strip and in the adjoining territories of Northern and Southern Rhodesia. It may therefore be expected to occur in the northern parts of the Protectorate too.

Probably of great economic importance is the fact that small animals, and especially birds, are suitable hosts for the larvae and nymphs. The birds often have a wide range of flight and may serve as carriers to other places, where the adults then find bigger hosts, including cattle and other domestic animals.

Amblyomma marmoreum Koch—Tortoise Tick.

Records.

SEROWE, 14.i.56—tortoise (not identified)—9 ♂♂, 3 ♀♀, 6 N.: TSESSEBE, 26.xii.55—*Gerrhosaurus validus*, Plated Rock Lizard—1 N.

Remarks.

This tick infests reptiles only and is of no medical or veterinary interest. It is the common Tortoise Tick of southern Africa, but it does not occur in East and Central Africa, as recorded by former authors. In the *marmoreum* group, many records are based on misidentifications, and these species are being reviewed by Miss L. E. Salisbury, Onderstepoort (Dr. G. Theiler, *in litt.*).

In some parts of the Union, the farmers persecute the tortoises in the false belief that the "bont tick" of these reptiles is identical with that found on cattle (*A. hebraeum*).

Haemaphysalis leachii leachii (Audouin)—Yellow Dog Tick.

Records.

KANYE, 16.xii.55—dog—7 ♀♀: MACHANENG MINES nr. KANYE, 17.xii.55—3 ♀♀: LEPHEPE, 18.i.56—dog—1 ♀.

Distribution.

Haemaphysalis l. leachii is quite common in the eastern Transvaal, in Swaziland, Zululand and Natal southwards to the Alexandria district; it is furthermore

fairly plentiful in certain places of the Western Province, for instance in the Swellendam, Worcester, Cape Town and Malmesbury areas. It is rare or absent in the more arid parts of the central and northern Transvaal, in the Orange Free State, Basutoland, Karroo and the Cape Plateau. It has not yet been found in the north-western Cape Province and South West Africa (Theiler & Robinson, 1953*a*).

H. l. leachii is an ubiquitous tick of tropical and southern Africa and is also known from the Yemen (Hoogstraal, 1956), but the records by former authors from the Oriental and Australian regions do not refer to this subspecies. The geographical records of its distribution do not give a clear picture of the ecological conditions favouring this species, since it is an ectoparasite of the dog and may find suitable climatic conditions on specific farms and native villages where it manages to maintain itself in very isolated and limited areas. This is probably also true for at least one record from the Protectorate. Kanye is situated in the parkland, where the conditions may still be naturally suitable for this tick; Lephepe, however, is a village in the Kalahari, where desert shrub predominates. It is interesting to note that only one female of *H. l. leachii* was collected from a dog, whereas five specimens of *Rhipicephalus simus simus* Koch, which can withstand much drier conditions, were present at the same time.

Host-specificity.

H. l. leachii is not common on dogs in the Protectorate and is greatly outnumbered by *R. simus simus*. In the Union, *H. l. leachii* has occasionally been found on the domestic cat too, but whether the immature stages infest wild carnivores and rodents in addition to the dog, is still an open question. Larvae and nymphs of the two subspecies of *H. leachii* are not yet clearly separable from each other, so the nymphs from the rodents and the larva from *Turdoides*, listed under *H. leachii muhsami* Dias, may belong partly, or as a whole, to *H. leachii leachii*. Theiler & Robinson (1953*a*) write that " the immature forms of the variety have not been bred under laboratory conditions, so that we are not in a position to state categorically that the immature stages of *H. leachi* do not feed on wild carnivores. The main evidence is against them doing so, for the wild carnivores and their tick variety are present throughout South Africa extending even into more arid areas, whereas the distribution of *H. leachi* does not follow that of the ubiquitous dog ".

Economic importance.

It has been known for several years (see Gear & De Meillon, 1941; Gear, 1954) that *H. l. leachii* harbours the causal agent of tick-bite fever (*Rickettsia conori*), and that domestic rats, and also field rats like *Rhabdomys pumilio* and *Otomys irroratus*, are natural reservoirs of the disease. They are commonly infested with larvae and nymphs of *H. leachii* ssp. which may also infest humans. It seems likely, therefore, that at least some of the immature specimens of *H. leachii* found on field rats belong to the ssp. *leachii* and not exclusively to the ssp. *muhsami*.

To the veterinarian, this species of tick is known as a transmitter of biliary fever of dogs caused by *Babesia canis*. This disease has evidently not yet been reported from the Protectorate (Director of Vet. Services, by letter).

Haemaphysalis leachii muhsami Dias—Lesser Carnivore Tick.

Records.

FRANCISTOWN, 18.xii.54—*Paraxerus cepapi*, Yellow-footed Squirrel—8 ♂♂, 2 ♀♀, 1 N. (Dias, 1955*c*): BOSOLI,* 3.i.56—*Genetta genetta felina*, Small-spotted Genet—heavily infested with adult ticks: Nr. TOTENG (Lake Ngami),

* Between Francistown and Tsessebe.

4.i.55—*Suricata suricatta*, Suricate—1 ♂, 4 N., 1 L. (Dias, 1955*c*): TSAU, 8.i.55—*Thos mesomelas*, Black-backed Jackal—1 ♂ (Dias, 1955*c*).

The following immature specimens may belong partly or as a whole to *H. leachii leachii* (see also under that ssp.):

SEHITWA (Lake Ngami), 13.xii.44—*Desmodillus auricularis*, Namaqua Gerbil—several nymphs: Nr. TOTENG (Lake Ngami), 15.xii.44—*Tatera schinzi*, Schinz's Gerbil, and *Aethomys namaquensis*, Namaqua Rock-mouse—several nymphs: PALAPYE, 14.i.45—*Tatera schinzi*, Schinz's Gerbil—several nymphs: TSESSEBE, 2.i.56—*Turdoides jardinei*, Arrow-marked Babbler—1 L.

Remarks.

Dr. Theiler regards *muhsami* as a smaller and plumper variety of *H. leachii* and provisionally identified it as *H. leachii* near *indica* Warb. *H. leachii indica* itself is restricted to the Oriental region. According to Dr. Theiler, the morphological features of the adults overlap more or less, whereas the immature stages cannot be clearly separated at all. Dias (1955*b*) considers *muhsami* as a distinct species.

No special studies have been done on the geographical and ecological distribution of this subspecies, but it is known to inhabit also the drier parts of southern Africa, where the typical *leachii* is not found.

Nothing is known about the medical and veterinary significance of *H. leachii muhsami*, but it may be equivalent to that of the typical form.

Haemaphysalis hoodi hoodi Warburton & Nuttall—Eyeless Bird Tick.

Records.

MAUN, 23.xii.54—*Pternistis swainsoni*, Swainson's Francolin—4 ♂♂ (Dias, 1955*c*); 30.xii.54—*Centropus senegalensis*, Fleck's Coucal—2 ♂♂, 1 ♀ (Dias, 1955*c*); 30.xii.54—*Crecopsis egregia*, African Crake—1 ♀ (Dias, 1955*c*); 2.i.55—*Laniarius neglectus*, Grey-rumped Boubou—1 ♂ (Dias, 1955*c*).

Remarks.

This species seems to infest birds only and is widespread in Africa south of the Sahara, but probably prefers the warmer parts. In the Protectorate, it was only found near the swamps.

Nothing is known about its medical or veterinary importance.

Hyalomma rufipes Koch—Hairy Bont-legged Tick.

*Records.**

LOBATSI (abattoir), 31.i.56—cattle—moderately infested with adult ticks (see remarks under *Amblyomma hebraeum*): KANYE, 16.xii.55—cattle—1 ♂, 1 ♀; 16.xii.55—goat—1 ♀; 15.xii.55—*Afrotis afra*, Black Korhaan—1 L.; 13.vii.56—*Laniarius atrococcineus*, Crimson-breasted Shrike—5 N.: SEKHWAWA,† 8.x.55—cattle and horse—heavily infested: DEBEETE (quarantine camp), 20.xii.55—cattle—6 ♂♂, 1 ♀; 19 & 22.vii.56—*Lepus saxatilis*, Scrub Hare—many nymphs and larvae; (25 m. NW), 18.i & 19.vii.56—*Struthio camelus*, Ostrich—2 ♂♂, 2 ♀♀; (25 m. SE), 15.vii.56—*Francolinus sephaena*, Crested Francolin—1 N., many larvae; (25 m. SE), 20.i.56—*Bubo lactea*, Verreaux's Eagle Owl—7 L.; (25 m. SE), 26.vii.56—*Lamprotornis mevesii*, Long-tailed Purple Starling—3 N., many larvae; DEBEETE (quarantine camp), 20.xii.55—*Melittophagus pusillus*, Little Bee-eater—4 L.; 20.i.56—*Muscicapa striata*, Spotted Fly-catcher—5 L.; 15.vii.56—*Plocepasser mahali*, White-browed Sparrow-weaver—1 N., 2 L.; 20.xii.55—*Ploceus velatus*, Masked Weaver—1 N.: THABALE nr. SEROWE, 16.i.56

* See first footnote on p. 203.

† South-west of Kanye.

—cattle and horse—moderately infested with adult ticks: FRANCISTOWN (abattoir), 7.ii.56—cattle—6 ♂♂ (slight infestation); 18.xii.54—*Cuculus canorus*, European Cuckoo—2 L. (Dias, 1955*c*): BOSOLI*–TSESSEBE, 9.i.56 & 1/2.ii.56—cattle—strongly infested with adult ticks; 28.xii.55—*Lepus saxatilis*, Scrub Hare—6 N., 5 L.; 7.i.56—*Francolinus adspersus*, Red-billed Francolin—3 L.; 10.i.56—*Phoeniculus purpureus*, Red-billed Hoopoe—5 N.; 25.xii.55—*Rhinopomastus cyanomelas*, Scimitar-bill—heavily infested with larvae; 23.xii.55—*Pycnonotus xanthopygos*, Black-capped Bulbul—1 L.; 9.i.56—*Hirundo rustica*, European Swallow—6 N.; 3.i.56—*Dicrurus adsimilis*, Fork-tailed Dongo—8 L.; 10.i.56—*Tchagra australis*, Brown-headed Tchagra—1 ♀, 6 N.; 25.xii.55—*Poliospiza gularis*, Streaky-headed Seed-eater—1 N.: MAUN, 30.xii.54—*Centropus senegalensis*, Fleck's Coucal—1 N. (Dias, 1955*c*): TSAU, 6 & 8.i.55—*Equus burchellii*, Burchell's Zebra—strongly infested with adult ticks (Dias, 1955*c*).

Distribution.

According to the above listed records, the area of distribution of *H. rufipes* in the Protectorate seems to coincide with that of *Amblyomma hebraeum*, but this is doubtless due to inadequate collecting. From the Union and other parts of Africa (Hoogstraal, 1956), it is known to withstand extremely dry conditions and may extend into regions with a rainfall of 20–25 in. (508–635 mm.), which, in moister years, would even include the area of Ghanzi. However, it cannot be concluded that this species of tick exists permanently or temporarily in this district, because it is not the rainfall itself which is the deciding factor, but the vegetation, which is dependent on the rainfall, in combination with the kind of soil and also other factors.

H. rufipes is also recorded from non-Ethiopian regions, namely from the Mediterranean and the U.S.S.R. There is no doubt that it was originally an Ethiopian species, and was probably brought to these parts of the world by migrating birds (see below).

Many of the old records concerning the distribution are unreliable owing to confusion with other species.

Host-specificity.

H. rufipes infests a wide range of mammals and birds and normally behaves as a two-host tick. However, in certain cases it may also behave as a three-host tick. Hosts of the adults are normally bigger mammals like cattle, horses, sheep, goats and certain wild ungulates, whereas, according to Hoogstraal (1956), antelopes are less common hosts. The immature stages may also be found on these hosts, and the species seems to behave then as a three-host tick, but normally the larvae and nymphs feed on small mammals and especially on birds, which is clearly indicated also by the records from the Protectorate.

Economic importance.

Of great interest and economic importance is the fact that the immature stages of this tick readily attach themselves to birds, many of which may serve, as in the case of *Amblyomma hebraeum*, as carriers to other places. The Russian author Pomerantsev (1950) believes, for instance, that the presence of *H. rufipes* in the U.S.S.R. is due to small local populations established from nymphs from migrating birds.

With respect to the medical importance, nymphs of *H. rufipes*, taken from a hare in the Union, were found to be infected with the causal agent of tick-bite fever (*Rickettsia conori*). Curiously enough, it has not yet been proved to be a vector of an animal disease, but like *H. truncatum* Koch, it may be involved in transmitting sweating sickness. Its bites, however, are severe and may cause

* Between Francistown and Tsessebe.

abscesses and sloughing of the skin in domestic animals. The wounds caused by the bites of the ticks often enable the screw-worm, *Chrysomyia bezziana* Villen., to penetrate the skin. This fly is very common in certain parts of the Protectorate, especially in the north. Furthermore, the tick may be associated with footrot of sheep caused by a secondary bacterial infection, and also with lameness in sheep.

Hyalomma truncatum Koch—African Bont-legged Tick.

*Records.**

Lobatsi (abattoir), 31.i.56—cattle—moderately infested with adult ticks: Kanye, 16.xii.55—cattle and goat—1 ♂ each; 22.i.56—*Papio comatus*, Chacma Baboon—3 L.; 16.xii.55—*Pternistis swainsoni*, Swainson's Francolin—heavily infested with larvae; 15.xii.55—*Creatophora cinereus*, Wattled Starling—5 L.: Sekhwawa,† 8.x.55—cattle—a few males: Nr. Sekhuma, 25.i.55—*Oryx gazella*, Cape Oryx—5 ♂♂, 2 ♀♀ (Dias, 1955*c*): Debeete, 20.xii.55—cattle—1 ♂; (25 m. SE), 20.i.56—*Alcelaphus caama*, Red Hartebeest—1 N.: Debeete (25 m. SE), 18.vii.56—*Strepsiceros strepsiceros*, Greater Kudu—1 ♂; (25 m. SE), 19.xii.55—*Coracias garrulus*, European Roller—4 L.: Serowe, 14.i.56—tortoise (not identified)—2 ♂♂, 2 ♀♀: Thabala nr. Serowe, 16.i.56—cattle—4 ♂♂, 2 ♀♀,—horse—3 ♂♂, 3 ♀♀: Motshegalatan nr. Serowe, 16.i.56—cattle—1 ♂, 5 ♀♀: Francistown (abattoir), 7.ii.56—cattle—3 ♂♂, 1 ♀; pig—1 ♂: Tsessebe, 2 & 9.i.56—cattle—7 ♂♂, 11 ♀♀; 9.i.56—*Strepsiceros strepsiceros*, Greater Kudu—1 ♂; 3.i.56—*Ciconia ciconia*, White Stork—3 L.; 6.i.56—*Coracias caudata*, Mailikazi's Roller—2 L.: Nr. Toteng (Lake Ngami), 11.i.55—*Struthio camelus*, Ostrich—1 ♂ (Dias, 1955*c*): Tsau, 6 & 8.i.55—*Equus burchellii*, Burchell's Zebra—8 ♂♂, 1 ♀ (Dias, 1955*c*); 9.i.55—*Syncerus caffer*, Buffalo—1 ♂ (Dias, 1955*c*).

Distribution.

H. truncatum (=*transiens* Schulze) is found only in the Ethiopian region and commonly occurs in the drier parts, but is rare or absent in the forests of western Africa (Hoogstraal, 1956). In the Bechuanaland Protectorate it is probably present throughout, as in South West Africa and the adjoining districts of Hay and Gordonia (Dr. Theiler, *in litt.*).

Host-specificity.

H. truncatum was often confused by former authors with *H. rufipes* or identified as *H. aegyptium* (L.), a species which is actually a tortoise parasite and restricted to the southern Palaearctic. The data available from the Protectorate and also from other parts of Africa (see Hoogstraal, 1956) are too few, or based on doubtful identifications, so that no conclusions can be drawn about differences in the ecology or host-specificity of *H. truncatum* and *H. rufipes*. As in the case of *H. rufipes*, birds and small mammals evidently play an important rôle as hosts and carriers of the immature stages, whereas the adults prefer cattle and other big ungulates. The presence of several adults on a tortoise at Serowe is certainly only incidental and not of any significance.

Economic importance.

A male of *H. truncatum* (identified as *H. transiens*) was shown to have caused paralytic symptoms in a male European in the Transvaal (Erasmus, 1952). The tick, cited as *H. aegyptium*, which was mentioned by Gear (1954) as harbouring the causal agent of tick-bite fever (*Rickettsia conori*) in southern Africa, is

* See first footnote on p. 203.

† South-west of Kanye.

actually *H. truncatum*. Like many other ticks, it was also found to be infested with *Coxiella burneti* (Q fever).

Neitz (1954) recently proved that *H. truncatum* is a transmitter of sweating sickness of cattle. Like *H. rufipes*, it inflicts severe bites which may give rise to abscesses and other secondary infections and enable the screw-worm, *Chrysomyia bezziana*, to penetrate the skin.

Rhipicephalus appendiculatus Neumann—Brown Ear Tick.

Records.

LOBATSI (abattoir), 31.i.56—cattle—♂♂ and ♀♀ about as frequent as *A. hebraeum*: DEBEETE (25 m. SE), 18.vii.56—*Strepsiceros strepsiceros*, Greater Kudu—3 ♂♂, 1 ♀: THABALE nr. SEROWE, 16.i.56—cattle—10 ♂♂, 12 ♀♀; 16.i.56—horse—1 ♂, 1 ♀: FRANCISTOWN (abattoir), 7.ii.56—cattle—very heavily infested with adults; sheep—1 ♂, 7 ♀♀; pig—1 ♂, 2 ♀♀: TSESSEBE, 2.i.56 & 1.ii.56—cattle—2 ♂♂, 3 ♀♀,—dog—1 ♂: BOSOLI,* 4.i.56 & 9.i.56—*Strepsiceros strepsiceros*, Greater Kudu—heavily infested with adults: MAUN, 16.ii.56—cattle—7 ♂♂, 5♀♀: Nr. TOTENG (Lake Ngami), 4.i.55—*Suricata suricatta*, Suricate—4 L. (Dias, 1955*c*): TSAU, 9.i.55—*Syncerus caffer*, Buffalo—1 ♂, 1 ♀ (Dias, 1955*c*); 6 & 8.i.55—*Equus burchellii*, Burchell's Zebra—1 ♂, 1 ♀ (Dias, 1955*c*).

Distribution.

R. appendiculatus is widespread in the Union and is common in the moister parts of the east and the south (forests and tall grassland); it is present in all three types of parkland, but is rarer and more scattered; and it is absent from the short and mixed grass of the high- and middleveld as well as from all types of desert shrubs (Theiler, 1949*b*).

The records from the Protectorate coincide well with the findings in the Union. *R. appendiculatus* is present and common in the parkland of the east and in the savannah country of Ngamiland and the swamps. It was not found in the desert shrub of the Kalahari.

Host-specificity.

R. appendiculatus is a three-host tick. The adults are found predominantly on large mammals, especially on cattle and big wild ungulates. The nymphs and larvae may also be found on these big animals, but sometimes they also attach themselves to smaller mammals, and in the laboratory, the whole life-cycle may be completed on the domestic rabbit. Birds, however, are not suitable for any of the stages of this species of tick.

Economic importance.

R. appendiculatus is of considerable veterinary importance in South Africa as well as the tropical parts of East and Central Africa including the Belgian Congo, but it is absent from West Africa (Theiler & Robinson, 1954). It is the chief vector of East Coast fever (caused by *Theileria parva*), which is not known to occur in the Protectorate, but occasional epidemics have been reported from Southern Rhodesia and from various parts of the Union. Redwater in cattle, however, caused by *Babesia bigemina*, is not rare in the Protectorate and may be spread by *R. appendiculatus*. Most probably *Theileria mutans*, which is apathogenic in cattle or only causes mild reactions, also occurs in the Protectorate. *R. appendiculatus* is one of the proved vectors. With respect to its medical significance, *R. appendiculatus* has been found in the Union to be infected with the causal agent of tick-bite fever (*Rickettsia conori*).

In East Africa, the virus of Nairobi sheep disease is transmitted by *R.*

* Between Francistown and Tsessebe.

appendiculatus, and it has been proved experimentally that the louping-ill of sheep in Great Britain is also transmissible by this tick.

Rhipicephalus distinctus Bedford—Dassie Brown Tick.

Records.

TSESSEBE, 2.i.56—*Procavia capensis*, Rock Dassie—1 ♂.

Remarks.

Rhipicephalus distinctus is one of the few ticks showing a strict host-specificity, which may, however, be primarily determined by the unique ecological conditions of the habitat of its host, the rock dassie.

So far, *R. distinctus* is not known to have any medical or veterinary significance.

Rhipicephalus evertsi evertsi Neumann—Red-legged Tick.

*Records.**

KANYE, 16.xii.55—cattle—1 ♀,—goat—7 ♂♂, 3 ♀♀, 1 N.; 22.i.56—*Papio comatus*, Chacma Baboon—2 L.: SEKHWAWA,† 8.x.55—cattle—moderately infested,—goat—moderately infested: DEBEETE (quarantine camp), 20.xii.55—cattle—1 ♂; (25 m. SE), 23.vii.56—*Aepyceros melampus*, Impala—11 N., 16 L.; (25 m. SE), 20.i.56—*Raphicerus campestris*, Steinbok—4 N.: LEPHEPE, 25.vii.56—*Felis lybica*, Wild Cat—5 N.; 18.i.56—*Lepus saxatilis*, Scrub Hare—1 N.: MAHALAPYE, 14.i.45—*Lepus saxatilis*, Scrub Hare—several nymphs and larvae: THABALA nr. SEROWE, 16.i.56—cattle—1 ♂, 2 ♀♀,—goat—7 ♂♂, 1 N.: FRANCISTOWN, 7.ii.56—sheep—heavily infested with larvae and nymphs: BOSOLI,†† 2 & 9.i.56—cattle—20 ♂♂, 21 ♀♀; 9.i.56—*Strepsiceros strepsiceros*, Greater Kudu—1 N.; 26.xii.55—*Phalacrocorax africanus*, Reed Cormorant—4 L.; 10.i.56—*Tchagra australis*, Brown-headed Tchagra—7 N.: TSAU, 6–8.i.55—*Equus burchellii*, Burchell's Zebra—strongly infested with adults (Dias, 1955*c*).

Distribution.

R. evertsi evertsi is widely distributed throughout the Ethiopian region, including the mountains of Yemen (Hoogstraal, 1956). It tolerates a much greater aridity than *R. appendiculatus*; it is, however, absent from the Karrooveld of the Central Cape, from Bushmanland, Namaqualand and South West Africa. In the latter area, *R. evertsi evertsi* is replaced by the subspecies *mimeticus* Dönitz, which is probably more resistent to aridity than the nominate form. In northern Angola and the south-western Congo, the distribution areas of the two subspecies meet and overlap.

According to Theiler (1950*a*), who carried out a detailed study of the distribution of *R. evertsi evertsi* in southern Africa, this form is present in eastern Bechuanaland, but dies out westwards in the Kalahari desert. The records listed above seem to confirm this statement. I collected the subspecies *mimeticus* in the Outjo district of South West Africa (see Dias, 1955*a*), but not in the western part of the Protectorate. It would be interesting to detect the western limits for *evertsi*, *s. str.*, and the eastern limit for *mimeticus*, and to compare the ecological conditions.

Host-specificity.

According to Hoogstraal (1956), "adult red ticks most commonly occur on domestic cattle, equines, goats and sheep, and on wild antelopes, zebras and a

* See first footnote on p. 203.

† South-west of Kanye.

†† Between Francistown and Tsessebe.

few other large game animals. If a comparative host-predilection study of this species could be undertaken, it is likely that domestic horses, mules, and donkeys and wild zebras might rank highest as preferred hosts". "Immature stages normally feed on the same type of large-size host as do the adults, though their feeding sites on the animal differ markedly. Under some conditions, larvae and nymphs attack hares, elephant shrews, tree rats, and baboons, but the factors causing these presumably atypical infestations are not known." The records from the Protectorate seem to indicate that the infestation of small mammals and especially of hares may not be as atypical as Hoogstraal believes, whereas birds are probably only incidental hosts of the immature stages.

R. evertsi is a two-host tick, meaning that the larva and nymph feed on the same host specimen. An interesting fact is that the adults are normally attached in the perianal region under the base on the tail, less commonly on the teats, at the base of the legs, or on the scrotum. The immature stages are mostly found deep in the depressions of the inner ear surface.

Economic importance.

R. evertsi evertsi is of great veterinary importance and known to be capable of transmitting the following diseases: East Coast fever (*Theileria parva*), pseudo East Coast fever (*Theileria mutans*), redwater (*Babesia bigemina*), biliary fever in horses (*Babesia equi*), and spirochaetosis, caused by *Borrelia theileri*, in various domestic stock. Of these diseases, only redwater is recorded from the Protectorate.

According to Hoogstraal (1956), *R. evertsi evertsi* also harbours the causal agent of tick-bite fever (*Rickettsia conori*).

Rhipicephalus oculatus Neumann—Hare Tick.

Records.

DEBEETE, 19.xii.55—*Nasilio brachyrhynchus*, Short-snouted Elephant Shrew—1 N., 7 L.: PALAPYE, 14.i.45—*Lepus saxatilis*, Scrub Hare—several larvae: TSESSEBE, 28.xii.55—*Lepus saxatilis*, Scrub Hare—1 L.

Remarks.

R. oculatus is a typical parasite of hares, which harbour all three stages of this tick. Shrews are often infested with the immature stages, but only incidentally with adults. Other animals, notably goats and cattle, are occasionally infested. The tick is known from most of the drier parts of the Union, from South West Africa, Angola, Southern Rhodesia and Kenya (Theiler & Robinson, 1953*b*).

According to Theiler (*in litt.*), it has been shown that *R. oculatus* is able to transmit East Coast fever (*Theileria parva*) and gall sickness (*Anaplasma marginale*).

Rhipicephalus pravus Dönitz—False Brown Tick.

Records.

KANYE, 16.xii.55—goat—1 ♀: DEBEETE, (25 m. SE), 18.vii.56—*Strepsiceros strepsiceros*, Greater Kudu—1 N., 1 L.; (25 m. SE), 23.vii.56—*Aepyceros melampus*, Impala—1 N.; (25 m. SE), 20.vii.56—*Raphicerus campestris*, Steinbok—1 ♂, 2 ♀♀; (quarantine camp), 19.vii.56—*Lepus saxatilis*, Scrub Hare—1 ♂, 1 N., 1 L.; (quarantine camp), 19.vii.56—*Nasilio brachyrhynchus*, Short-snouted Elephant Shrew—very heavily infested with larvae and nymphs: LEPHEPE, 18.i.56—*Lepus saxatilis*, Scrub Hare—3 ♂♂, 5 ♀♀: MAHALAPYE, 19.i.45—*Lepus saxatilis*, Scrub Hare—infested with adults and nymphs: PALAPYE, 14.i.45—*Lepus saxatilis*, Scrub Hare—infested with adults: TSESSEBE,

9.i.56—cattle—1 ♀; 23.xii.56—dog—1 ♂, 1 ♀; 4 & 9.i.56—*Strepsiceros strepsiceros*, Greater Kudu—20 ♂♂, 23 ♀♀: Tsessebe, 28.xii.55—*Lepus saxatilis*, Scrub Hare—2 ♂♂, 1♀: Tsau, 8.i.55—*Equus burchellii*, Burchell's Zebra—1 ♀ (Dias, 1955*c*, under *R. neavei*).

Distribution.

The specificity of this tick has only been recognised since the last World War. It was formerly confused with other species, mainly *R. appendiculatus* and the Palaearctic *R. bursa* Can. & Fanz. According to Theiler & Robinson (1953*b*), it is widely distributed over South Africa and even reaches Angola and the

Map 3.—● = *Rhipicephalus sanguineus* (Latreille).

Cameroons in the west, but it evidently prefers the drier parts. In the Union, it occurs mainly in the " Bushveld or dry Parklands; it avoids open grass lands or the more humid Parklands. It occurs in areas with seasonal rainfall alternating with fairly long dry periods, and with rainfall above 10 inches and below 25 inches. It appears to be relatively frost resistant. being firmly established in areas with over 90 days frost per annum."

Host-specificity.

R. pravus, a three-host tick, infests a wide range of mammals, but preferred hosts for the adults are the herbivores, with hares as second choice. The immature stages seem to prefer smaller animals, especially hares and shrews.

Economic importance.

R. pravus has been shown experimentally to be capable of transmitting East Coast fever (*Theileria parva*).

Rhipicephalus sanguineus sanguineus (Latreille)—Kennel Tick.

Records. (See map 3.)

MACHANENG MINES nr. KANYE, 17.xii.56—dog—1 ♀: SEKHUMA, 25.i.55—*Oryx gazella*, Cape Oryx—3 ♂♂, 2 ♀♀ (Dias, 1955*c*): TSANE, 20.i.55—*Alcelaphus caama*, Red Hartebeest—1 ♂ (Dias, 1955*c*): DEBEETE (25 m. SE), 20.i.56—*Vulpes chama*, Chama Fox—1 ♂; (20 m. NW), 27.vii.56—*Ardeotis kori*, Giant Bustard—1 ♀; (20 m. NW), 18.i.56—*Struthio camelus*, Ostrich—2 ♂♂: LEPHEPE, 18.i.56—dog—1 ♂; 18.i.56—*Lepus saxatilis*, Scrub Hare—2 ♂♂: THABALA nr. SEROWE, 16.i.56—goat—1 ♂,—horse—1 ♀: FRANCISTOWN, 7.ii.56—cattle—2 ♂♂, 1 ♀: BOSOLI,* 9.i.56—cattle—16 ♂♂, 16 ♀♀; 23.xii.55 & 3.i.56—dog—1 ♂, 4 ♀♀; 4.i.56—*Strepsiceros strepsiceros*, Greater Kudu—1 ♂: MAUN, 30.xii.54—*Orycteropus afer*, African Ant-bear—1 ♂ (Dias, 1955*c*): TSAU, 6.i.55—*Equus burchellii*, Burchell's Zebra—1 ♂ (Dias, 1955*c*); 8.i.55—*Thos mesomelas*, Black-backed Jackal—3 ♂♂, 2 ♀♀ (Dias, 1955*c*).

Distribution.

R. sanguineus is not restricted to the Ethiopian region, but is found today as an ectoparasite of man or of his dog in all warmer parts of the world.

There is no paper dealing with the distribution of the Kennel Tick in the Union, and the records obtained from the Protectorate are somewhat confusing. It was found, but always in relatively small numbers, in Tsessebe and Francistown in the lowveld area as well as in Tsane, Sekhuma and Lephepe in the dry Kalahari.

Host-specificity.

The hosts infested range from the dog and jackal to various kinds of antelope, and even big birds appear occasionally as suitable hosts. It is possible that dogs and wild Canids are mainly responsible for this wide distribution, transporting the tick to places with quite different ecological conditions, but that the dropped ticks are easily capable of infesting other animals too.

Economic importance.

The economic importance of this cosmopolitan tick is quite pronounced. *R. sanguineus* is a well-known vector of tick-bite fever (caused by *Rickettsia conori*) in Africa south of the Sahara as well as in the Mediterranean and the U.S.S.R. In North America, it was also found to transmit the causal agent of Rocky Mountain spotted fever (*Rickettsia rickettsi*) and tularaemia (*Pasteurella tularensis*). In Australia, *R. sanguineus* was found infected with Q Fever

* Between Francistown and Tsessebe.

(*Coxiella burneti*), and in North Africa it is an occasional transmitter of relapsing fever, caused by *Borrelia hispanica*.

To the veterinarian, this tick is known to be the vector of canine biliary fever (caused by *Babesia vogeli* and *B. gibsoni*) and the rickettsiosis of dogs, caused by *Rickettsia canis*. It also transmits the apathogenic *Hepatozoon canis* in Africa. In North America, *R. sanguineus* is one of the transmitters of anaplasmosis of cattle; in the U.S.S.R., it has been proved to transmit *Babesia equi* and *B. caballi* among horses.

Rhipicephalus simus simus Koch—Glossy Brown Tick.

Records.

LOBATSI (abattoir), 31.i.56—cattle—1 ♀: KANYE, 18.i.56—dog—13 ♂♂, 4 ♀♀: MACHANENG MINES nr. KANYE, 17.xii.55—dog—15 ♂♂, 4 ♀♀: DEBEETE (25 m. SE), 20.i.56—*Vulpes chama*, Chama Fox—3 ♀♀; (quarantine camp), 19.vii.56—*Lepus saxatilis*, Scrub Hare—1 N.: LEPHEPE, 18.i.56—dog—3 ♂♂, 2 ♀♀: THABALA nr. SEROWE, 16.i.56—horse—1 ♀,—dog—2 ♀♀: FRANCISTOWN (abattoir), 7.ii.56—cattle—6 ♂♂, 5 ♀♀; 17.ii.56—pig—1 ♂: BOSOLI,* 2. & 9.i.56—cattle—16 ♂♂, 27 ♀♀; 23.xii.55 & 3.i.56—dog—28 ♂♂, 26 ♀♀; 3. & 9.i.56—*Strepsiceros strepsiceros*, Greater Kudu—4 ♂♂, 2 ♀♀; 26.xii.55—*Phalacrocorax africanus*, Reed Cormorant—1 ♀: Nr. NATA, 26.xii.44—*Hystrix africae-australis*, Cape Porcupine—1 ♂: TSAU, 8.i.55—*Equus burchellii*, Burchell's Zebra—1 ♂ (Dias, 1955*c*); 8.i.55—*Thos mesomelas*, Black-backed Jackal —2 ♀♀ (Dias, 1955*c*).

Distribution.

Rhipicephalus simus simus is found practically all over the Ethiopian region; in West Africa it is more or less widely replaced by the subspecies *senegalensis* Koch. A detailed study of the distribution in the Union has not yet been published. In southern Africa, it probably finds the most suitable conditions in the bush and the parkland formations, but may be brought by dogs and wild Canids to the drier parts too, as indicated by the infestation of dogs in Lephepe.

Host-specificity.

R. simus simus is a three-host tick which, like *R. sanguineus*, infests a wide range of mammals. The hosts selected by the adults are carnivores, including the domestic dog, which, for instance in the Protectorate, is more commonly infested with this tick than with the true dog-ticks, *Rhipicephalus sanguineus* and *Haemaphysalis leachii*. According to Hoogstraal (1956), the buffalo and pigs are also favourite hosts, whereas antelopes are "usually second-choice hosts". It is important to note that humans are frequently attacked by the adult ticks, especially in the vicinity of their dwellings. Larvae and nymphs feed chiefly on burrowing rodents, less commonly on hares and other small mammals. The occurrence of a female tick on a cormorant at Bosoli is certainly only an incidental one. Dr. Theiler informs me (*in litt.*) that this "record for an adult off a bird is the only one I have thus far—otherwise I have but three records of immatures off birds".

Economic importance.

Rhipicephalus simus simus has been accused of occasionally causing tick paralysis in man (Zumpt & Glajchen, 1950). In Africa, it is a proved vector of East Coast fever, caused by *Theileria parva*, of redwater (*Babesia bigemina*), of piroplasmosis of pigs (*Babesia trautmanni*), and of gall sickness (*Anaplasma marginale*).

* Between Francistown and Tsessebe.

Rhipicephalus theileri Bedford & Hewitt—Theiler's Brown Tick.

Records.

Nr. TOTENG (Lake Ngami), 4.i.55—*Suricata suricatta*, Suricate—1 ♂ (Dias, 1955*c*).

Remarks.

This is a very rare species, originally described from the South African Ground Squirrel, *Geosciurus inauris.* Nothing is known about its medical or veterinary importance.

Rhipicephalus tricuspis Dönitz—Lesser Glossy Brown Tick.

Records.

KANYE, 16.xii.55—goat—1 ♂, 3 ♀♀; 15.xii.55—*Afrotis afra*, Black Korhaan—1 ♀: SEKHUMA, 25.i.55—*Oryx gazella*, Cape Oryx—14 ♂♂, 9 ♀♀ (Dias, 1955*c*): DEBEETE (20 m. SE), 20.i.56—*Alcelaphus caama*, Red Hartebeest—3 ♂♂, 10 ♀♀; (20 m. SE), 20.i.56—*Raphicerus campestris*, Steinbok—25 ♂♂, 5 ♀♀; (20 m. SE), 20.i.56—*Vulpes chama*, Chama Fox—very heavily infested with adults: LEPHEPE, 18.i.56—*Sylvicapra grimmia*, Grey Duiker—3 ♂♂; 18.i.56—*Lepus saxatilis*, Scrub Hare—2 ♂♂: BOSOLI,* 2.i.56—cattle—1 ♀; 23.xii.55 & 3.i.56—dog—1 ♂, 4 ♀♀; 9.i.56—*Strepsiceros strepsiceros*, Greater Kudu—1 ♂: MAUN, 30.xii.54—*Orycteropus afer*, African Ant-bear—12 ♂♂, 1 ♀ (det. *lunulatus* Neumann, Dias, 1955*c*): TSAU, 8.i.55—*Thos mesomelas*, Black-backed Jackal—2 ♂♂, 3 ♀♀ (det. *lunulatus* Neumann, Dias, 1955*c*).

Distribution.

R. tricuspis (=*lunulatus* Neumann, according to Theiler, see Hoogstraal, 1956) has a scattered distribution throughout the Ethiopian region. It seems to be resistant to a wide range of humidity and aridity and may be found in areas with heavy rainfall (42 in. = 1,066·8 mm. annually) and also in those with a drought period lasting as long as seven months. In southern Africa, it occurs in the warmer parts from the semi-arid bushveld of the Kalahari to the moister lowveld of the Transvaal and Natal.

Host-specificity.

Immature stages of this species have not yet been recorded from hosts under natural conditions, but Dr. Theiler (in press) has succeeded in rearing *R. tricuspis* in the laboratory. The adults are found mainly on larger animals, either domestic or wild. In the Protectorate, *R. tricuspis* does not appear to be a rare species on antelopes and wild carnivores, and a Chama Fox shot near Debeete was found to be exceptionally heavily infested with this tick. The female found on a korhaan at Kanye is the first record from a bird, but the infestation must be regarded as an incidental one.

Economic importance.

According to Hoogstraal (1956), *R. tricuspis* is suspected of being a transmitter of porcine piroplasmosis (*Babesia trautmanni*).

Boophilus decoloratus (Koch)—Blue Tick.

Records.

LOBATSI (abattoir), 31.i.56—cattle—7 ♀♀, 1 N.: KANYE, 16.xii.55—cattle—2 ♀♀: SEKHWAWA,† 8.x.55—cattle—moderately infested with all stages:

* Between Francistown and Tsessebe.
† South-west of Kanye.

Debeete (25 m. SE), 18.vii.56—*Strepsiceros strepsiceros*, Greater Kudu—1 L.; (25 m. SE), 23.vii.56—*Aepyceros melampus*, Impala—2 L.: Thabala nr. Serowe, 16.i.56—horse—1 ♂, 3 ♀♀: Motshegalatan nr. Serowe, 16.i.56—cattle—9 ♀♀: Francistown (abattoir), 7.ii.56—cattle—1 ♂, 13 ♀♀: Bosoli,† 9.i.56—*Strepsiceros strepsiceros*, Greater Kudu—15 N.; 26.xii.55—*Phalacrocorax africanus*, Reed Cormorant—2 L.: Maun, 16.ii.56—cattle—1 ♂, 2 ♀♀.

Distribution.

Boophilus decoloratus is distributed throughout most of the Ethiopian region, where it prefers the more humid areas, but avoids the dense tropical rain-forests. In southern Africa (Theiler, 1949*a*), the most important factor in limiting its spread is increasing aridity, the critical level being represented by an annual rainfall below 15 in. (=381 mm.). This fact explains its rareness and scattered occurrence in the Protectorate. As one of the most common cattle ticks in more humid areas of the neighbouring territories, it is certainly very often imported with cattle, but it has difficulty in becoming established or dies out again during the periods of drought.

Host-specificity.

B. decoloratus is a one-host tick and a typical parasite of cattle and large game. Smaller mammals are rarely found infested with this tick, and the finding of 2 larvae on a cormorant at Bosoli must be regarded as quite unusual. Most probably these larvae would not have been able to complete their life-cycle on such an unsuitable host.

Economic importance.

This tick is of great veterinary significance. It is one of the most important transmitters of redwater (caused by *Babesia bigemina*), probably also of European redwater (caused by *Babesia bovis*), and of anaplasmosis (caused by *Anaplasma marginale*). These three diseases are recorded from the Protectorate. Furthermore, *B. decoloratus* is a transmitter of *Borrelia theileri* among cattle, horses, sheep and goats. Heavy infestations of *B. decoloratus* may lead to an acute anaemia in cattle and horses.

B. decoloratus has been accused of harbouring the causal agent of tick-bite fever (*Rickettsia conori*), but this remains to be proved and is highly improbable.

Argas persicus (Oken)—Fowl Tampan.

Records.

Kanye, 15.xii.55—native huts—common: Francistown, 20.xii.55—native huts—common: Tsessebe, 9.i.55—native huts—common.

Remarks.

A. persicus feeds mainly on fowls and is found almost everywhere in the warmer parts of the world. Occasionally, it has also been found parasitising wild birds. During the night, natives in the Protectorate often keep their chickens inside the huts, where crevices provide ideal hiding places for the ticks. *A. persicus* readily inflicts painful bites on man, but does not transmit any disease to him. The natives often confuse this tick with the Eyeless Tampan (*Ornithodoros moubata* (Murr.)), which is a true parasite of man.

A. persicus transmits spirochaetosis of fowl (caused by *Borrelia anserina*) and fowl piroplasmosis, caused by *Aegyptianella pullorum*.

† Between Francistown and Tsessebe.

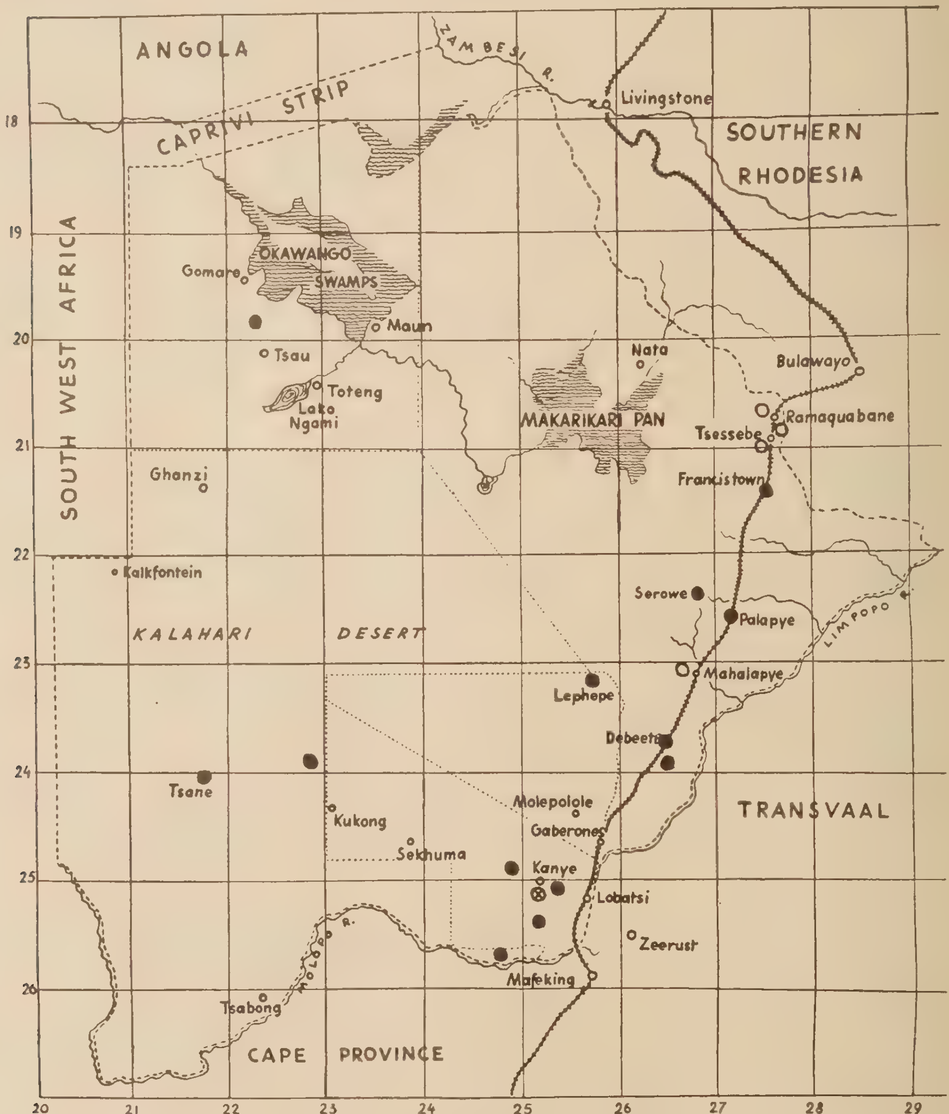
Argas vespertilionis (Latreille)—Bat Tampan.

Records.

DEBEETE, 20.i.56—*Bubo lactea*, Verreaux's Eagle Owl—1 L.

Remarks.

The common bat tampan of southern Africa is *Argas confusus* Hoogstraal (see Hoogstraal, 1956), which was confused with *A. vespertilionis* by former authors. The finding of a larva of the true *A. vespertilionis* was quite unexpected for two



Map 4.—*Ornithodoros moubata* (Murray).

⊗ = found infected with *Borrelia duttoni*; ● = found, not infected; ○ = not found.

reasons, firstly, because *A. vespertilionis* is a rare species in southern Africa, and secondly, because an owl was found infested. The explanation is probably that the owl was attacked by this parasite in its hiding place, where the true hosts, namely bats, were also present.

Adults and nymphs of these species of *Argas* occasionally bite man, when they invade the rooms of a bat-infested house.

Ornithodoros moubata (Murray)—Eyeless Tampan.

Records.

On the trip in December 1955–January 1956, a great number of native huts were examined for *O. moubata* in the following localities:

Kanye, Sesu,* Sekhwawa,† Machaneng,* Linchwe,** Lephepe, Mahalapye, Palapye, Serowe, Thabala and Motshegalatan nr. Serowe, Francistown, Tsessebe, Ramaquabane and several farms and isolated huts between Francistown and the Rhodesian border. Huts at Bojankwe, Ngamiland, were examined by Mr. Davis in March 1944, and those of Mabule (nr. Majaning ††) and Kong (nr. Tsane) just recently by the Medical Services of the Protectorate. The results of these examinations are indicated on map 4.

Distribution.

The distribution of *O. moubata* in the Protectorate and the neighbouring South West Africa is still confused. The records mentioned by Leeson (1952), and the map of distribution drawn by him, are based partly on misidentifications, owing to the confusion of this species with *O. savignyi* (Aud.) and *Argas persicus*, and are therefore worthless. Walton (1955) has shown that *O. moubata* is quite irregularly distributed in Kenya. The reasons for this remain obscure and may be dependent upon ecological as well as social conditions. The same seems to be true for the Protectorate and for South West Africa. *O. moubata* was found in the area between Kanye and Francistown. Of all villages checked in this district, Mahalapye was the only one in which no ticks were found. This finding, however, is not conclusive, since owing to shortage of time and to the reluctance of the Damara population, it was only possible to examine four huts. The area north of Francistown, on the other hand, seems to be free of *O. moubata*, for a great number of huts in Tsessebe and Ramaquabane, as well as isolated huts from the Rhodesian border down to the farms near Bosoli, were very carefully checked and no tampans were found.§ It must be mentioned that the standard of life of the natives in that region is exceptionally high and their huts are clean and well kept. It is doubtful, however, whether this factor alone or in conjunction with ecological conditions could be responsible for the absence of *O. moubata*. In Tsessebe, a few huts were found to be infested with *A. persicus*, which also bites man and normally causes a more severe skin reaction than does *O. moubata*. The tampans which a native of Bosoli said had infested his hut several years ago were most probably fowl tampans.

The detection of *O. moubata* in native huts is not an easy matter, since the ticks hide during the day in crevices in the floor and walls. In one case, an old hut was superficially checked and no ticks found. However, when the hut was completely pulled down, large numbers of ticks were found hiding in holes in the wall.

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* Near Kanye.

† South-west of Kanye.

** South-east of Debeete.

†† North-west of Mafeking.

§ Later investigations carried out by a team of workers of the Medical Services in Bechuanaland have shown that *O. moubata* does occur in this area. Failure to find it was probably due to the fact that the huts had previously been sprayed with insecticides as a mosquito control measure.

Host-specificity.

Formerly, man was regarded as the chief host of *O. moubata*, but it was known, too, that this tick also readily attacks domestic pigs and fowl living with or in the vicinity of humans. In the laboratory, *O. moubata* can easily be reared on rats, rabbits and guineapigs, which indicates that no pronounced host-specificity has been developed.

The question has often been discussed whether man is the original host of this tick, or, which is more probable, whether he acquired this parasite from some wild African mammals. A relatively recent discovery is the finding of *O. moubata* in the burrows of the wart-hog (*Phacochoerus aethiopicus*), the ant-bear (*Orycteropus afer*) and of porcupines (*Hystrix* sp.) in various parts of Africa. It was not possible to examine burrows of these animals in the Protectorate. A pangolin (*Smutsia temminckii*), however, killed by natives at Debeete on 26.vii.56, was found to be infested with several nymphs of *O. moubata*. This animal was also found to harbour *O. moubata* in southern Mozambique (Dias, 1951).

Economic importance.

Under natural conditions, *O. moubata* is normally the only transmitter * of *Borrelia duttoni*, the causal agent of relapsing fever in Africa. From a medical point of view it is therefore the most important tick in the Bechuanaland Protectorate. Earlier assertions that *O. savignyi* may also transmit this disease have been cast into considerable doubt by subsequent research.

The specimens collected in the Protectorate were brought alive to the South African Institute for Medical Research, Johannesburg, and were tested by Dr. D. Ordman for infectivity with *Borrelia duttoni*. Only one batch, from Kanye, was found to be infected. Of the 20 ticks tested, 1–3 were infected (5–15%). Records in this Institute, however, show that relapsing fever in humans has been reported from the following places: Lobatsi, Gaberones, Molepolole, Mahalapye, Serowe, Francistown and Maun. Occasional epidemics of relapsing fever are therefore to be expected in all places where *O. moubata* is found.

It is claimed that some specimens of *O. moubata* collected in Ruanda-Urundi are naturally infected with *Rickettsia burneti* (Q Fever) and that others from the Kivu district have been found infected with an organism referred to as "Bashi virus-rickettsia" (see Hoogstraal, 1956).

When *O. moubata* feeds on fowl, it may become infected with *Borrelia anserina* (fowl spirochaetosis) and *Aegyptianella pullorum* (fowl piroplasmosis) and may also act as a vector among the birds.

Ornithodoros savignyi (Audouin)—Sand Tampan.

Records.

Nr. Wagdraai,† at Molopo River, December 1956—numerous adults and nymphs.

These specimens were collected from sand in stock yards between Werda and Bray, and were sent in by the Director of Medical Services.

Remarks.

O. savignyi occurs in the arid parts of North, East and South Africa, the Near East, India and Ceylon. It probably had its original home in the East, and invaded Africa from there (Hoogstraal, 1956). Its exact distribution within this range is not yet known, owing to lack of field research and to confused identifications.

O. savignyi has a predilection for resting in the soil under trees. According

* Heisch (1950) has found that, in East Africa, the body louse (*Pediculus humanus humanus* L.) may also be naturally infected with *Borrelia duttoni*.

† South-west of Sekhuma.

to Hoogstraal (1956), camels are most frequently mentioned as hosts, but fowls and domestic animals may also be attacked. Domestic animals may even be killed by the volume of blood lost when attacked by numbers of tampans. Human beings are frequently bitten, and the bite may have extremely painful *sequelae*. This tampan has never been found infected with pathogenic organisms in nature.

Summary.

Twenty one species of ticks (IXODOIDEA), one of which is represented by two subspecies, are recorded from the Bechuanaland Protectorate. Localities, dates and the hosts are given; general distribution and medical and veterinary importance are discussed under each species.

The shrub desert formations of the Kalahari are shown to be unsuitable habitats for most species of ticks; only a few are able to survive under severe desert conditions.

In medical respects, *Ornithodoros moubata* (Murr.), as the transmitter of relapsing fever, is the most important tick in the Protectorate. It has been found in the eastern part up to Francistown and in Ngamiland and near Tsane; its further distribution has not yet been established. Larvae and nymphs of various members of the IXODIDAE infesting domestic and wild rodents are potential transmitters of tick-bite fever.

Cattle in the eastern area and in Ngamiland were found to be infested by ten species, of which *Amblyomma hebraeum* Koch, *Hyalomma rufipes* Koch, *H. truncatum* Koch, *Rhipicephalus appendiculatus* Neumann, *R. evertsi evertsi* Neumann, *R. simus simus* Koch and *Boophilus decoloratus* (Koch) are the most important ones, both in respect of the numbers infesting cattle, and of their significance as transmitters of redwater, anaplasmosis, heartwater and sweating sickness. [a disease of unknown etiology affecting cattle (protracted

Sheep, goats, pigs and horses were found to be infested by nine of the species listed above as occurring on cattle.

Dogs were mainly parasitised by *Rhipicephalus simus* which outnumbered by far the two recognised dog-ticks, *Rhipicephalus sanguineus sanguineus* (Latr.) and *Haemaphysalis leachii leachii* (Aud.).

Wild Bovids and zebra are infested by species which also live on domestic ruminants, but the percentage of the different species present varies according to the host and to the locality.

Wild carnivores are infested by the same species as are dogs, but in this group, too, there are differences in the relative abundance of the various tick species.

Small birds are hosts of immature stages of *Amblyomma* and *Hyalomma* species. Their importance as carriers for the dispersal of cattle-infesting ticks is noticed.

Acknowledgements.

The identification of the material was undertaken by Dr. G. Theiler and Miss L. E. Salisbury of the Division of Veterinary Services, Onderstepoort, and by Dr. J. A. Travassos Santos Dias, Missão de Combate às Tripanossomíases, Tinonganine, Mozambique. I wish to thank all persons and authorities mentioned above for their help and interest, especially Dr. G. Theiler for her advice and criticism of the manuscript.

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THE AVAILABILITY OF *GLOSSINA MORSITANS* WESTW. IN ANKOLE, UGANDA.

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In Ankole district of southern Uganda, fly-rounds were set up to determine the availability of *Glossina morsitans* Westw. Two areas were chosen, one at Kamalia, which lies at 0°21′S. latitude, 30°58′E. longitude, and the other on the edge of Lake Mburo, 19 miles south of Kamalia.

The vegetation of the two areas is similar and consists largely of well-grown *Acacia hebecladoides* woodland with *A. seyal* var. *multijuga*. Small termite-mound thickets, dominated by *Rhus glaucescens*, are common.

The object was to discover if there were differences in the availability of *G. morsitans* in this type of woodland and in the *Brachystegia–Isoberlinia* woodland of Tanganyika where much work has been carried out on this species by the late Dr. C. H. N. Jackson. The standard availability (East Africa High Commission, 1950, p. 22) is the proportion of the fly population appearing to the catching party when 10,000 yd. of linear catches are done in each square mile of fly belt. As Buxton (1955, p. 452) observes "this figure is extremely valuable, for it enables one to relate fly-round data (so simple to collect) to population studies". He goes on, however, to point out some of its limitations. The method of calculation is given in the Appendix.

Methods.

A fly-round path was set out in each area in the form of a grid of paths laid parallel to each other and 250 yd. apart. The legs were joined, forming a continuous path, which was 7,000 yd. long at Kamalia and 5,000 yd. at Mburo. Catching stations were at 100-yd. intervals along these paths. It was intended that these fly-rounds should sample an area in the same way that a spiral fly-round does.

Flies were individually marked, using the 25,000 mark-system (Jackson, 1953), and released again from December 1954 to May 1955 at Kamalia and from July to October 1955 at Mburo. Population estimates were calculated by extrapolation from recaptures (Jackson, 1939, 1948 & 1953). The area sampled by each fly-round was taken as the actual area covered by the grid of paths, to which was added an extra 100 yd. on each side except where, at Mburo, the fly-round passed close to the lake shore. At Kamalia this area was 0·54 sq. mile and at Mburo 0·40 sq. mile.

All observations refer to non-teneral males, that is, to male flies that have fed at least once since emergence.

Results.

In both areas the number of recaptures was low, due to low availability. At Kamalia, it proved possible to obtain two reasonable estimates of the population, the first over the period from mid-December 1954 to mid-February 1955, and the second from mid-April to early June 1955 (for details see Appendix). For the first period the estimate was 2,670 non-teneral males per square mile with fiducial

limits of 1,850 and 4,800. For the second period the estimate of 8,380 non-teneral males per square mile was rather higher. The fiducial limits were 5,170 and 22,000. The apparent density (the number of non-teneral males caught per 10,000 yd.) during the first period was 36·9, hence the availability was between 2·0 and 0·77 per cent. For the second period the apparent density was 43·0, giving a standard availability between 0·83 and 0·19 per cent.

At Mburo, all data from the three months of operation were combined to obtain one estimate of 12,400 non-teneral males per square mile, with fiducial limits of 7,700 and 30,800. The apparent density was 80·1 during this period, hence the availability was between 1·03 and 0·26 per cent. As the three estimates of the standard availability from Ankole overlap, there is no significant difference between them.

Discussion.

Jackson gives the standard availability of *G. morsitans* in the *Brachystegia–Isoberlinia* woodland at Kakoma, Tanganyika, as 13 per cent. from data covering a complete year (Jackson, 1944), though later it appeared that this estimate was rather high and the new figure of 10 per cent. was calculated (East Africa High Commission, 1950, p. 22). Also, from the data given in his paper on Gedamara, Tanganyika, in *Acacia–Combretum* woodland (Jackson, 1953) the standard availability from the population estimates calculated by the extrapolation method has a mean, over three months, of 12·6 per cent. The two estimates agree well and are considerably greater than those obtained in Ankole.

A standard availability of 10 per cent. means that one non-teneral male caught per 10,000 yd. is equivalent to a population of approximately 10 non-teneral males per sq. mile. Taking the highest and lowest of the fiducial limits from the Ankole work, 2·0 and 0·19 per cent., we find that one non-teneral male per 10,000 yd. is equivalent to a population of between 50 and 526 non-teneral males per sq. mile. The difference between the Ankole estimates and the Tanganyika ones is most marked and is of great practical significance. In the past we have tended to think that Jackson's estimates of standard availability probably applied in Ankole but it is now apparent that the single fly found after long search there is of considerably more importance than hitherto thought. This is the probable explanation of the trypanosomiasis problem round the edges of the fly-belt in Ankole when patrols yielded very few, or no, flies. It also means that, after the bush has been cleared, intensive observations such as fly-rounds or patrols must be kept running for a long period before one can be sure that the fly population has died out.

The low availability in Ankole might be explicable if the flies were particularly well adapted to their environment; this interpretation is supported by the population estimates which are very high compared with those from Tanganyika (655 non-teneral males per sq. mile at Kakoma and 320 per sq. mile at Gedamara). However, flies did not appear to be unusually well adapted according to other means of observing this, namely hunger and female and teneral percentages. Also, while game was abundant and apparently readily available as hosts, it was not more so than at Gedamara.

The estimate of availability may be influenced by various factors such as the method of catching, frequency of stops, time of day, temperature and visibility in the woodland. The author had the good fortune to be present while much of Jackson's Gedamara work was in progress and believes the conditions to have been reasonably similar in the two places. The Gedamara block, however, was isolated and apparently no immigration or emigration took place. This was not the case in Ankole, where the areas concerned formed part of a large fly-belt, and so the exact area sampled by the fly-rounds is open to doubt; but the subspecies

was the same in both areas, namely *G. morsitans morsitans* Westw., and it is considered that the estimates from the two areas are comparable.

Summary.

Two areas in Ankole, Uganda, were studied with a view to obtaining estimates of the standard availability of *Glossina morsitans* Westw. These estimates gave maximum and minimum fiducial limits of 2·0 and 0·19 per cent. These are considerably lower than the estimates, obtained by Jackson in Tanganyika, of approximately 10 per cent. This difference is of practical importance in that a single fly caught in Ankole indicates a much larger population, and this is the probable explanation of the trypanosomiasis problem round the edges of the fly-belt, where routine catches showed flies to be scarce.

Acknowledgements.

I am grateful to Mr. J. Ford, Dr. J. P. Glasgow and Dr. E. Bursell for their assistance and encouragement during this work and to Mr. D. L. Johns for helpful discussion.

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Appendix.

Numerical Results.

Recaptures of non-teneral males of *G. morsitans* at Kamalia, from 13th December 1954 to 19th February 1955, by weeks.

Week of recapture	Total captures	Week of release 1	2	3	4	5	6	7	8	9
2	151	22								
3	136	6	8							
4	173	9	9	5						
5	192	2	4	6	10					
6	142	2	2	0	6	11				
7	143	2	0	3	1	2	4			
8	103		0	0	1	0	3	4		
9	71			0	0	2	0	0	1	
10	121				1	2	0	1	3	5
	Initial releases :	190	129	122	150	170	121	131	93	64

Recaptures of non-teneral males of *G. morsitans* at Kamalia, from 18th April to 4th June 1955, by weeks.

Week of recapture	Total captures	Week of release 19	20	21	22	23	24
20	212	9					
21	147	3	3				
22	183	1	4	4			
23	230	2	5	1	5		
24	140	0	2	2	1	2	
25	157	0	1	2	1	0	2
	Initial releases :	190	201	140	172	215	129

Recaptures of non-teneral males of *G. morsitans* at Mburo, from 29th July to 14th October 1955, by weeks.

Week of recapture	Total captures	Week of release 1	2	3	4	5	6	7	8	9	10	11	12
2	219	4											
3	98	2	1										
4	118	0	1	2									
5	252	1	7	1	2								
6	203	0	0	1	0	6							
7	223	2	0	0	0	5	5						
8	191		0	0	0	2	1	3					
9	152			0	0	1	0	1	1				
10	147				0	0	0	0	3	2			
11	142					0	0	2	2	1	4		
12	192						0	1	1	0	3	3	
13	36							0	0	0	0	0	2
	Initial releases :	153	212	93	115	240	196	208	185	149	140	126	184

In these Tables, flies recaptured for the second, third, etc., time are shown on each occasion against the date of their initial release only, and opposite the date of each recapture.

The recapture figures were corrected to the values that would have been expected had the numbers of captures and releases been exactly 100. The resulting figures were then summed in each of the six rows running from NW to SE and the means taken, giving six values of y, y_1 to y_6, reading horizontally from right to left.

The extrapolated point, " a ", was calculated from the following formula:

$$a = \frac{(y_1+y_2+y_3+y_4+y_5)^2}{(y_2+y_3+y_4+y_5+y_6)} - (y_1+y_2+y_3+y_4)$$

Then the population $= \frac{10^4}{a}$.

The standard error of " a " was calculated from the formula (Jackson, 1939):

$$S^2 = a\,A_1\,f\,(r)$$

and the result multiplied by 2·25.

The standard availability % $= \frac{\text{Apparent density} \times 100}{\text{Population per square mile}}$, where the apparent density is the number of non-teneral males caught per 10,000 yd.

THE CHEMICAL CONTROL OF THE WATTLE BAGWORM, *KOTOCHALIA JUNODI* (HEYL.), BY AERIAL SPRAYING.

II.—THE USE OF TOXAPHENE AND ENDRIN IN THE EARLIER STAGES OF AN INFESTATION.*

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An exploratory large-scale experiment in aerial spraying was conducted in 1953, when plantations of wattle (*Acacia*) infested with larvae, up to the third instar, of the bagworm, *Kotochalia junodi* (Heyl.), were treated with toxaphene in light diesel oil (Ossowski, 1954, as *Acanthopsyche*). At the time of spraying, the infestation had entered the first year of its eruptive stage and the overall density of the larval population was consequently very high. It was, however, unevenly distributed over the plantation, a fact which significantly influenced the results obtained. Where the population was dense, the results were poor; a high kill resulted only where the infestation was light. In order to procure more detailed information on the effect of insecticides on less dense populations, another experiment was carried out in the Wartburg district in 1956, when the infestation was in the first year of the premonitory stage and the population light throughout the whole area. Toxaphene and endrin were used, the latter having given promising results in small-scale experiments (Ossowski, 1956*a*).

Material and Methods.

Plot lay-out and description.

The plantations in which the experiment was carried out were established between 1951 and 1953 and carried 410 to 450 trees to the acre. The average height of the trees was 40 ft. and that of the crowns 25 ft., with an average area at the base of the crown of nearly 90 sq. ft. Taking into consideration the various types of crowns in the plots (classes 1 and 2a to 2d of the British Forestry Commission), the average crown volume was approximately 750 cu. ft. The canopy was even throughout all plots. The average number of larvae per tree was 40, with a maximum of little more than 200. A randomised block arrangement comprising four replications of each treatment was used, each block consisting of six plots of approximately 5 acres each (572 yd. × 42 yd.). The demarcation of the plots to be sprayed was carried out as described elsewhere (Ossowski, 1954), except that only corner flags were used.

Selection of sample trees and methods of sampling.

This was done as in the earlier experiment (Ossowski, 1954). The assessment of bagworm mortality started ten days after spraying and was completed in four days. At the time of assessment, 12 per cent. of the larvae were in their first instar, 29 per cent. had reached the second, and 59 per cent. the third.

Insecticides and method of application.

Each insecticide was dissolved in light diesel oil, endrin at the rate of 0·67 oz. and toxaphene at 0·75 lb. per gal. of solution. The former was sprayed at 3 gals.,

* An account of preliminary investigations on methods and organisation for large-scale aerial experiments was given in Ossowski (1954), which is now regarded as Part I of this series.

and the latter at 2, 3, 4 and 8 gals. per acre. Thus the actual amounts of insecticide were 2 oz. of endrin and $1\frac{1}{2}$, $2\frac{1}{4}$, 3 and 6 lb. of toxaphene per acre.

The aircraft used was a 150-H.P. Piper Super Cub P.A. 18A, equipped with 46 spray nozzles with D8 orifices and with a tank holding 90 gals. The load of insecticide was either 30 or 40 gals., according to the number of plots to be treated in one run. The plane, flying at 80 m.p.h., used a pressure of 15 lb. per sq. in. to apply 2 gals., 25 lb. per sq. in. to spray 3 gals., and 40 lb. per sq. in. to apply 4 gals. per acre. During operations, the pilot was in constant touch by radio with the entomologist in charge of operations.

In the experiment conducted in 1953, many of the hydrogen-filled marker balloons burst shortly after coming into contact with the spray. In the present experiment, therefore, vivid pink flags mounted on telescopic aluminium poles were hoisted halfway across the plots and between the two corner flags, thus indicating to the pilot not only the plot to be sprayed, but also the width of the swathe. Before commencing to discharge the insecticide, the pilot made a trial run over each plot to get his bearings. As the nominal swathe width was approximately 20 yd., the plane had to make two runs to cover each plot. All plots were treated in this way, except the 8-gal. toxaphene plots, which were sprayed twice at the rate of 4 gals. per acre, as the plane was unable to discharge the spray at a higher rate. In all, eleven flights were made. The experiment started on 16th November at about 5.30 p.m., but only four plots were sprayed on that day due to bad visibility. During the flights, the sky was overcast and the velocity of the wind approximately 2 m.p.h. The temperature was 14°C., with a relative humidity of 84 per cent. On the following day, spraying was resumed at 5.20 a.m. and was completed by 9.0 a.m. On this day, the temperature at the start was 14°C. and rose to 21°C. by 9.0 a.m.; the mean relative humidity throughout operations was 79 per cent. The sky was clear and there was no wind during spraying except for the last two plots, when a slight breeze arose. All plots received a good cover. A total of 3·37 in. of rain, fairly evenly distributed, fell during the 14 days during which the plots were under observation. The velocity of the wind during sampling was never more than 2 to 4 m.p.h., except on the second day after spraying, when a gale of over 30 m.p.h. blew for some three hours.

Results and Discussion.

Of the 20 sample trees in each treatment, the kill was complete on one tree sprayed with 2 gals. toxaphene solution per acre, on ten with 3 gals. and with 8 gals. toxaphene, and on eleven with 4 gals. toxaphene and with 3 gals. endrin.

TABLE I.

Mortality of bagworms 10–14 days after treatment.

Treatment	Total mortality (%)		Mean corrected kill
	Range over 4 replicates	Mean	
Unsprayed	18·8– 25·9	22·5	—
Toxaphene : 2 gals. ($1\frac{1}{2}$ lb.)/acre	68·5– 88·0	81·0	75·5
„ 3 „ ($2\frac{1}{4}$ lb.)/ „	96·5–100·0	97·3	96·6
„ 4 „ (3 lb.)/ „	93·9–100·0	98·1	97·5
„ 8 „ (6 lb.)/ „	96·8–100·0	98·9	98·5
Endrin : 3 „ (2 oz.)/ „	93·2–100·0	96·9	96·0

Standard error 2·38.
Significant difference (P = 0·05) 7·17.
Significant difference (P = 0·01) 9·92.

Two gals. of toxaphene solution per acre gave a significantly lower kill ($P = 0{\cdot}05$) than did the remaining treatments, which did not differ among themselves (Table I).

The mean kill in all treated plots was less in the lower parts of the crowns than in the upper ones (Table II), probably due to incomplete penetration of the insecticide, the difference being 20·6 per cent. with 2 gals. toxaphene solution and from 8·1 to 13·1 per cent. in the remaining treated plots. In the untreated plots the position was reversed, due mainly to parasitism by the white fungus, *Isaria psychidae* Pole Evans, which requires for its development a degree of humidity such as is more usually found in the lower, more shaded parts of the crowns.

TABLE II.

Mortality (excluding " fall-off ") in the upper and lower parts of crowns.

Treatment	Mean of 4 replicates (%)	
	Upper	Lower
Unsprayed	16·9	37·5
Toxaphene : 2 gals./acre	81·1	60·5
" 3 " "	98·5	88·8
" 4 " "	98·3	85·2
" 8 " "	98·4	90·3
Endrin : 3 " "	97·3	85·2

To collect the small fauna which fell from the trees, 120 ground sheets (one sheet per sample tree) were laid out, but material could be gathered from only 61, since the remainder were stolen. There was no difference in the final percentage " fall-off " of bagworms between the treated plots, but it was very much higher than in the untreated (Table III). Those treated with endrin showed a higher initial proportion, which suggests a more rapid toxic effect of this insecticide.

TABLE III.

Mean percentage " fall-off " of bagworms per tree at intervals after spraying.

Treatment	24 hr.	2 days	3 days	5 days	10–14 days	Total
Unsprayed control	0·12	0·15	0·14	0·19	0·13	0·73
Toxaphene: 2 gals./acre	1·15	1·44	2·30	1·40	0·06	6·35
" 3 " "	1·18	1·30	2·06	1·43	0·23	6·20
" 4 " "	1·12	1·46	2·01	1·20	0·11	5·90
" 8 " "	1·14	1·41	2·09	1·21	0·23	6·08
Endrin: 3 " "	1·60	2·01	2·25	0·16	0·17	6·19

In all treated plots the percentage fall-off was highest on the third day after treatment, due undoubtedly to the gale on the previous day.

Of other fauna, 7 specimens were collected from 15 sheets, covering 22·5 sq. yd., in the control plots, but the number found in the treated plots on 46 sheets of an area of 69 sq. yd., was 334. Of these, at least 214, equivalent to over 15,000 per acre, were beneficial to wattle plantations. All the arthropods other than bagworms found on the sheets are listed in Table IV by Orders and Families and also classified into groups according to their economic status.

Specimens belonging to the Hymenoptera, Diptera and Coleoptera, which were on the wing during spraying, were found on the sheets 10 to 15 minutes later, but most of these insects and nearly all the members of the Araneae were collected 24 hours after spraying. Very young Lepidopterous larvae were found on the

TABLE IV.

Classification and economic importance of arthropods (other than bagworms) found on sheets after spraying.

Order	Family	Number of specimens			
		Beneficial	Indifferent	Harmful	Total
(a) Unsprayed control plots (15 sheets)					
Hemiptera	Pentatomidae	1	0	0	1
Lepidoptera	Lasiocampidae	0	0	3	3
Coleoptera	Cleridae	1	0	0	1
Diptera	Asilidae	0	2	0	2
Total		2	2	3	7
(b) Sprayed plots (46 sheets)					
Orthoptera	Acrididae	0	0	5	5
Hemiptera	Cicadellidae and Miridae	0	0	10	10
	Pentatomidae	28	0	0	28
Lepidoptera	Lasiocampidae	0	0	20	20
	Noctuidae	0	0	4	4
Coleoptera	Cleridae	6	0	0	6
	Chrysomelidae	0	0	13	13
	Melolonthidae	0	0	41	41
Hymenoptera	Ichneumonidae	70	0	0	70
	Chalcididae	18	0	10	28
	Braconidae	7	0	0	7
	Apidae	21	0	0	21
Diptera	Tachinidae	31	0	0	31
	Asilidae	0	3	0	3
	Bibionidae	0	14	0	14
Araneae	Salticidae	21	0	0	21
	Argiopidae	5	0	0	5
	Clubionidae	7	0	0	7
Total		214	17	103	334

sheets two days after spraying, while later instars dropped two to three days later. Examples of the Hemiptera and Orthoptera were collected five to 14 days after spraying operations.

The experiment has confirmed that, under favourable weather conditions, a very high mortality can be obtained with endrin and toxaphene solutions when lower population densities are involved, but even a very high and uneconomic application of the latter insecticide (6 lb. in 8 gals. solution per acre) did not

give a kill sufficient to reduce the bagworm population to its endemic level.* This is probably due to incomplete penetration of the canopy, the killing of a very large number of beneficial members of the wattle fauna of small arthropods, and the very high biotic potential of bagworms, amounting to well over 99 per cent. (Anon., 1954).

It has already been noted (Anon., 1956) that where such partial control occurs, the cycle is interrupted, the peak delayed for one or even more years, and the infestation carried over at a dangerous level into the next season. Nevertheless, the result may be economically advantageous in terms of a single season by preventing trees from being defoliated, with consequent loss of increment.

Summary.

Replicated sample plots of wattle (*Acacia*) were sprayed from the air with 2 oz. endrin and $1\frac{1}{2}$, $2\frac{1}{4}$, 3 and 6 lb. toxaphene per acre, each in light diesel oil, to test the effect of these insecticides on the bagworm, *Kotochalia junodi* (Heyl.), and other wattle fauna. All invertebrates which fell from the sample trees were collected on sheets at intervals after spraying and identified. The mortality of bagworms was assessed after 10 to 14 days.

The mean corrected mortality was significantly lower in the treatment with $1\frac{1}{2}$ lb. toxaphene than in the others, which, however, did not differ significantly amongst themselves. In all cases the kill was greater in the upper than in the lower parts of the tree crowns. There was no difference in the final percentage "fall-off" of bagworms in all plots, though in those treated with endrin the initial rate was higher. A very high kill, ranging from 96·6 to 98·5 per cent., was obtained in all but the $1\frac{1}{2}$ lb. toxaphene plots, but even the 6 lb. application was not sufficient to reduce the bagworm population to its endemic level.

The arthropods, other than bagworms, collected on ground sheets are listed by Orders and Families and also classified into groups as beneficial, indifferent, and harmful. Nearly two-thirds of the total were found to be beneficial.

Acknowledgement.

Grateful acknowledgement is made of the untiring assistance rendered by Mr. John Gibson, of the Windy Hill Wattle Co. Ltd., and his field staff during the organisation and execution of the experiment.

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* The endemic level of a bagworm population depends on the age of the wattle plantation and climatic conditions. It cannot be expressed empirically, but is less than the lowest category of infestation (Ossowski, 1956*b*), *i.e.*, very few bagworms on occasional trees throughout the plantation.

THE PREFERENCE SHOWN BY *MYZUS PERSICAE* (SULZ.) FOR *BRASSICA* PLANTS SPRAYED WITH WETTING AGENTS.

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Insecticide formulations for spraying crops usually contain agents to disperse the insecticide and improve the wetting of the foliage. During a series of experiments to study the response of Aphids to leaves sprayed with insecticide, it was noticed that more Aphids often occurred on leaves which had been sprayed with a solution of wetting agent than occurred on unsprayed leaves. This paper gives evidence from these experiments for wetting agents seeming to attract Aphids, and describes other experiments done specifically to investigate the question.

Materials.

The plants used were either (1) cauliflower seedlings (var. Extra Early Roscoff) grown in small pots and used when they had 4 to 6 leaves, or (2) turnip seedlings (var. Early Six-weeks) in the 3- to 4-leaf stage.

The wetting agents tested were: 1. Lissapol N (Imperial Chemical Industries Ltd.); an alkyl aryl ethylene oxide condensate, non-ionic. 2. Sulphonated laurol (lauryl sodium sulphate); anionic. 3. Cyclohexylamine dodecyl sulphate; cationic. 4. Atlox 3335 (Atlox Powder Co.); a mixture of an anionic (an alkyl aryl sulphonate) with a non-ionic (polyoxyethylene sorbitan esters of mixed fatty and resin acids) wetting agent. All were in aqueous solution.

Aphids tested were winged and wingless adults of *Myzus persicae* (Sulz.), reared in a heated greenhouse and starved for at least two hours.

Methods.

Plants were sprayed " to run-off " with a paint sprayer operated by compressed air and were allowed to dry. Six plants were placed in a circle within a cage (cubical, with sides about 15 in.) which was then filled with peat to a level just above the rims of the pots, and the surface covered with white sand. Usually, two plants would have been sprayed with an insecticide, two with a solution of the wetting agent and two unsprayed. Aphids were released at the centre of the circle of plants, and the cage was slowly rotated to prevent Aphid movement being influenced by the direction of the light. The Aphids on each plant and the numbers of nymphs which they deposited were counted daily at approx. 9.30 a.m. The experiment continued until the insecticide had become ineffective.

Results.

Aphids are thought to recognise suitable food-plants only after probing the leaf surface with their probosces (Kennedy, 1950), and the Aphids in our experiments showed no powers of finding their food-plants by either sight or smell; walking Aphids moved in a more or less straight path and frequently they passed within two inches of an untreated food-plant without turning towards it; winged Aphids did not settle preferentially on either sprayed or unsprayed plants. The initial infestation was therefore random, and the ultimate population on different

plants indicated the subsequent movement from plant to plant, with the highest population occurring on preferred plants from which fewer Aphids moved.

It was the distribution of nymphs at the end of some of the experiments with insecticides that first indicated the preference of Aphids for plants sprayed with wetters. This is illustrated in Table I, which gives the results of three experiments with plants sprayed with Lissapol N or Toxaphene. Two plants received each treatment in all three experiments.

TABLE I.

Mean numbers of nymphs of *M. persicae* deposited on cauliflower seedlings during three cage experiments.

Expt.	Duration of expt. (days)	Lissapol N (0·1%)	Untreated	Toxaphene (0·1%)
1	10	41·5	19·0	13·5
2	5	19·5	2·0	1·0
3	5	28·0	1·0	0·5

Statistically significant evidence for the preference of Aphids for foliage sprayed with 0·1 per cent. Lissapol N was obtained from an examination of the results of 16 experiments originally designed to show the residual properties of a number of different insecticides; as each experiment included plants sprayed with wetter only and also unsprayed plants, they provide an adequately replicated body of evidence on the effect of the wetter. The experimental procedure has been described above. Each experiment provided daily observations (the number varying from one experiment to another) of the number of adult Aphids on each of two sprayed and two unsprayed plants. These daily readings were averaged to give the mean number of Aphids per plant for each experiment. The 16 experiments were regarded as replicates and their results, weighted for the number of observations, were averaged. When an effective insecticide was used, the population in the cage declined very rapidly; the mean numbers of Aphids per plant were, therefore, low: 2·1 on unsprayed plants; 3·4 on plants sprayed with Lissapol N. The difference is significant at the 5 per cent. level (difference between log (10 Aphids + 1) for the two treatments, 0·21 ± 0·082).

To find if wetting agents had an effect when sprayed on other types of leaf, three turnip seedlings were sprayed with 0·1 per cent. Lissapol N, and were put in the cage with three unsprayed seedlings. Fifty wingless and 45 winged individuals of *M. persicae* were released and left for four days. The final distribution of Aphids is shown in Table II.

TABLE II.

Mean numbers of Aphids on turnip seedlings treated with Lissapol N and untreated.

	Winged adults	Wingless adults	Nymphs
Lissapol N	1·7	17·0	91·0
Untreated	1·3	10·7	63·0

As Lissapol N is a non-ionic wetting agent, experiments were done using cauliflower seedlings and 0·1 per cent. solutions of three other wetting agents of different types to see if they would have a similar effect (Table III). Two of

these were tested at the same time, and two untreated plants acted as controls against the action of both of them. Many more Aphids were found on the sprayed than on the unsprayed plants after a week.

TABLE III.

Mean numbers of Aphid nymphs on untreated cauliflower seedlings and on those sprayed with wetter, after one week.

Wetting agent	Treated plants	Untreated plants
Cyclohexylamine dodecyl sulphate (cationic) ...	37·0	7·5
Sulphonated laurol (anionic)	43·5	
Atlox 3335 (mixture, anionic and non-ionic) ...	27·5	9·5

Discussion.

Spraying with any of a range of wetting agents made leaves as different as the waxy smooth ones of cauliflower and the hairy ones of turnip more acceptable to Aphids than were unsprayed leaves. Whether this fact could have any practical implication is uncertain. Normally, plants would be sprayed with a wetting agent only in conjunction with an insecticide, which, if effective, would leave no Aphids to be affected. Also, in these experiments, the Aphids were given a choice between sprayed and unsprayed plants, whereas this would rarely happen in practice as the whole of a crop would be sprayed. It is possible that any effect would be beneficial when sprays are made to control the vectors of virus diseases, by encouraging the insects to settle rather than move from plant to plant, and therefore carrying infection to fewer plants.

Summary.

Winged and wingless individuals of *Myzus persicae* (Sulz.), when offered a choice between unsprayed cauliflower seedlings and seedlings sprayed with a 0·1 per cent. aqueous solution of Lissapol N (a non-ionic wetting agent), preferred Lissapol-treated plants. This effect was statistically significant.

Further experiments showed that Aphids similarly preferred treated turnip seedlings to untreated seedlings. The preference for sprayed cauliflower seedlings was also shown when an anionic, a cationic and a mixed wetting agent were used.

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THE CONTROL BY INSECTICIDES OF *BRONTISPA LONGISSIMA* (GESTRO) (COLEOPT., CHRYSOMELIDAE–HISPINAE) ON YOUNG COCONUT PALMS IN THE BRITISH SOLOMON ISLANDS.

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(Plates VII–XI.)

Contents.

Introduction.

Brontispa longissima (Gestro) (Pl. VII, fig. 1) is an elongate, narrow beetle about 7·5–10 mm. long and 2 mm. wide, and very flat as befits its habitat between the closely appressed leaflets of young coconut fronds. The thorax and a band about 1 mm. wide at the anterior end of the elytra is yellowish red, the remainder of the elytra being black; the relative extent of red and black in the coloration, however, is subject to great variation both in different territories and within the same locality; in Ontong Java the predominant form is much more extensively red, this colour often extending over the anterior half and also the tip of the

elytra; in the main group of the Solomon Islands the elytra are sometimes entirely black, and on San Cristobal specimens were found in which the whole insect was black.

It is this colour variation which has been responsible for a great deal of the unjustified splitting of the species which has unfortunately occurred, resulting in some confusion in nomenclature. The form occurring in the Solomon Islands has long been known as *B. froggatti* Sharp. Dr. J. L. Gressitt, however, who has made a special study * of the group, does not consider it distinct from *B. longissima*, which is the older name and must therefore stand. We therefore accept, as far as the Solomon Islands form is concerned, the arrangement of Lepesme & others (1947), placing *froggatti* Sharp as only a form (of doubtful validity) within the species *longissima* (Gestro).

The larva is dirty white and recognisable by a pair of calliper-shaped processes at the tip of the abdomen, which persists also in the pupa (Pl. VII, figs. 3 & 4). The eggs are brownish, elliptical, usually placed end to end in short rows, and surrounded by excreta and débris produced by the feeding activities of the adults (Pl. VII, fig. 2). For detailed descriptions of adults and immature stages of the insect the reader should refer to other works (*e.g.*, Pagden & Lever, 1935; O'Connor, 1940; Lepesme & others, 1947).

B. longissima is found throughout the Solomon Islands (including Ontong Java, Rennell and Santa Cruz), the New Hebrides, New Caledonia, New Britain, New Guinea and, if Lepesme's taxonomic grouping is correct, in Java and Celebes. Its economic importance varies from place to place. In the Solomon Islands it is undoubtedly the most serious pest of young palms; at a time when there were considerable areas of young palms it was estimated that damage to the value of £65,000 had been suffered in less than a decade on Lever's Estates alone (Tothill, 1929). In extreme cases it can completely arrest development of young palms (Pl. VII, fig. 1), and even kill them. If the replanting of coconuts, which is overdue in the Solomon Islands, takes place in the near future, comparable damage may be expected unless steps are taken to control the beetle or protect the young palms.

Nature of damage.

Both adults and larvae damage the leaflets of young unopened fronds by eating away the surface tissues in narrow, linear streaks usually running parallel up the long axis of the leaflet (Pl. VII, fig. 1; Pl. VIII, fig. 1). O'Connor (1940) considers that adults do more damage than larvae owing to the longer duration of this stage, but Tothill (1929) considered the larvae to be the more destructive. The insects live and feed only in fronds which are still tender and unopened, and the eggs are laid in the same place, so that all stages are well protected. When the frond opens, the adults leave it and seek another which is in the right stage. The narrow feeding scars then enlarge to form irregular necrotic areas which become brown and die (Pl. VIII, fig. 2), and in severe cases the fronds become somewhat shrivelled and ragged (Pl. X, fig. 2) and more or less large areas of the leaflets break off so that the foliage becomes partially skeletonised (Pl. VIII, figs. 3, 4), and its effective photosynthetic tissue may in extreme cases be reduced to virtually nothing (Pl. XI, fig. 1).

It is young palms up to four or five years old which usually suffer most heavily (Pl. XI). All the factors involved are not entirely clear but it is probable that the shorter interval between the opening of successive fronds on mature palms, and their larger size, contribute in large measure to their relative freedom from attack. A mature palm may be expected to produce a new frond every 4–5 weeks. In young palms, after the rapid emergence of the first half dozen or so seedling

* Since published—*Nova Guinea*, **8**, pp. 205–324, Dec. 1957.—Ed.

leaves, the fronds are produced considerably less frequently and over the first 4–5 years of its life a young palm will, on average, produce a new frond only once in every 6–7 weeks; under adverse conditions the interval may exceed 8 weeks (unpublished data, A.H.G.). Thus on a young palm there is never more than one frond vulnerable to attack at any one time, and there is usually an interval between the opening of consecutive fronds when there is not one at a vulnerable stage. This results in all immigrant beetles becoming concentrated on those palms which do have a vulnerable frond, and the relatively small size of the fronds renders the damage more devastating. In a mature palm the fronds are larger, and there may be more than one infested frond at any one time; so that although the number of beetles may be much greater, the damage is relatively less. The rate of frond production gradually speeds up after a palm is about 5 years old, and, by the time it is 8–10 years old, the palm will be producing new fronds at the normal interval of 4–5 weeks. It is significant that it is at this age that healthy, vigorous palms appear to achieve relative immunity to severe beetle attack.

Only occasionally in the Solomon Islands are mature palms attacked on a big enough scale to do serious damage. In one or two small areas near Honiara on Guadalcanal, however, this does occur, and at Lunga a number of palms are in a very poor state, and a very few have actually died, apparently as the result of *Brontispa* attack (Pl. VIII, fig. 4). Such a state of affairs is so rare, however, and the areas are so small that they would not justify the difficulty and expense which would be involved in trying to control such attacks. Despite the limited extent of serious damage, however, a few examples of *Brontispa* are to be found on a very high proportion of mature palms throughout the plantations. In the event of any new planting, and particularly in the case of replanting beneath existing stands of mature palms, this beetle population, though small, has proved sufficient to initiate a devastating attack on seedling palms. Since many plantations in the Solomon Islands are now past their prime, and a great deal of replanting is overdue, it is especially desirable at the present time to devise means of protecting young palms from attack.

Early attempts at control.

Insecticides.—Earlier insecticide methods tried included the shaking of a spray of soap and nicotine (obtained by boiling tobacco stalks) from beer-bottles with perforated corks on to the central spike of the palm (Lever, 1933). This does not seem to have been very effective and Tothill (1929) studied the method critically, and found it to be unsatisfactory on the grounds of expense, due to the labour involved. Later, some experiments were initiated with lead arsenate and bordeaux mixture (Lever, 1933, 1934); these were never completed, and the method was discouraged as likely to cause scorching of the foliage. In New Guinea, a spray fluid of nicotine sulphate ("Black-leaf 40") was poured down the central spike; Froggatt & O'Connor (1941) state that this usually killed adults and larvae, but that sometimes arsenate of lead had to be forced in with a spray pump.

We know of no published data indicating exactly how effective these earlier insecticidal methods were. In many cases the potential effectiveness of the insecticides themselves was probably not realised owing to the unsatisfactory methods of application that were employed.

Surgical methods.—Surgical methods were also tried, involving the cutting out and destruction of the central unopened frond which is the stage when it harbours the beetle. This has to be carried out over a large area at one time to reduce re-infestation from neighbouring palms, and has to be repeated fairly often to be effective, and it becomes a question of whether the palm can stand the loss of so much foliage. Tothill (1929) suggested that palms three to six years old

could stand the loss of one leaf every six months, but that younger palms could not as it would cause too great a check. Unless mature palms are also treated it will not greatly affect the *Brontispa* population as a whole, and Tothill points out how expensive the method can be, involving as it does much labour and extra European supervision if it is to be carried out with the necessary care. Surgical treatment cannot therefore be recommended.

Biological control.—It is only intended to review this subject very briefly here; further details can be found in the references cited. The Eulophid larval and pupal parasite, *Tetrastichus* (*Tetrastichodes*) *brontispae* (Ferrière), had been introduced in 1932 into South Celebes (where *Brontispa longissima* var. *selebensis* Gestro was doing severe damage) from Java, where it apparently kept in control the local form of *Brontispa*, presumably *B. longissima* var. *javana* Weise (Awibowo, 1934). It seems to have become established rapidly in Celebes and exercised control; further history of the introduction, and interesting biological data, are given by Franssen & Mo (1952). Lever (1935, 1936) introduced this same parasite into the Solomon Islands in 1936 and further consignments were imported in 1937 by Phillips. The wasps were bred up in confinement and liberated in large numbers on Ufa in the Russell Islands and on Guadalcanal. A method, later used in New Britain, for breeding up the parasite, is given by O'Connor (1940). There is no clear evidence as to the later history of these introductions into the Solomon Islands, but no spectacular effects occurred, possibly because little new planting was being undertaken; there were few young palms, and conspicuous damage, such as had been known in the 1920's, did not occur at the time of the introduction.

Vigorous attempts to introduce and establish *Tetrastichus* were also made at Lingatu from 1936 onwards. Here very optimistic reports of considerable lessening of beetle damage followed the earlier releases, and a few allegedly parasitised pupae were collected from the areas where releases were made. However, these improvements seem to have been either illusory or, at best, very short-lived as subsequent reports became increasingly pessimistic. In 1939 the Plantation Inspector reported that *Tetrastichus* must be considered to have failed as a means of combating *B. longissima*.

In 1940, a consignment of an egg parasite, *Trichogrammatoidea nana* (Zhnt.) was introduced from New Guinea and released on Lingatu Estate, but there are no indications that this parasite ever became established.

Towards the end of 1953, one of us (A.H.G.) decided to attempt to find out if *Tetrastichus* was still present on Ufa and whether or not there were any local parasites exercising any control over *Brontispa* that might be rendered effective if their populations could be increased.

Owing to the limited amount of time that could be spared for the work the results were inconclusive. Such as they were, the data failed to show any signs of parasites effectively attacking the beetle at any stage in its life-cycle.

The method of working was to collect all stages from the field and to keep them under observation in captivity. Eggs were kept until they hatched, or if they failed to do so in the normal time, for a further period of three weeks to see if any parasites emerged. Larvae were kept till they pupated or, if they failed to do so, for a period of three weeks after their death. Pupae and adults were treated in the same way. The specimens were inspected daily whenever possible and otherwise at intervals of not more than three days. Fresh coconut leaf was always provided as food.

There was a high mortality rate at all stages, but no parasites were found except in one egg. As numerous casualties also occurred in specimens bred entirely in captivity it must be concluded that many losses were due to faulty rearing technique. The method of keeping the insects in jars may have caused excessive humidity which could possibly be lethal.

The results that were obtained are summarised below:—

Stage	No. collected	No. attaining next developmental stage	No. parasitised
Egg	594	330	1*
Larva	1289	603	0
Pupa	614	537	0
Adult	586	—	0

* The parasite which emerged was sent to Fiji but could not be identified owing to its unsatisfactory state of preservation.

No attempt was made to carry out dissections of any of the specimens as a means of locating possible parasites.

It is strongly suggested by these observations that *Tetrastichus*, if it has survived at all, has not become established on Ufa in sufficient numbers to exercise control; the continued prevalence of *Brontispa* in the other localities where the parasite was introduced suggests that there, too, it has been unsuccessful. Further, no local parasites of any stage in the life-history appear to exist in numbers sufficient to exercise any control.

Susceptibility to Attack of different Varieties of Coconut.

In the course of the development of the plantations in the Russell Islands, seed nuts were obtained from a variety of sources.

The earliest plantings were made with nuts collected from palms in native coconut groves in various parts of the Protectorate. Later, about 1907, large numbers of nuts were imported from Samoa and a smaller quantity from Malaya.

It was reported that the three varieties differed in their susceptibility to *Brontispa* attack; and the Malayan palms were said to have suffered more severely than either the Solomon Islands or Samoan strains.

However, no experiments were carried out to measure the extent of this difference in susceptibility.

In 1953 the question arose—which variety should be chosen for some proposed replanting? In spite of the damage they had suffered when young, the original Malayan blocks had developed into some of the best producing areas in the plantations. Even where the output of copra per acre did not exceed that produced by the other varieties, the Malayan blocks could be worked more economically as the individual nuts were up to 30 per cent. larger so that less labour was required per ton of copra produced.

Was this advantage worth sacrificing in order to reduce the cost of *Brontispa* control in the early years? With the prospects of successful chemical control still uncertain, it was decided to carry out a varietal resistance trial to compare the extent of damage suffered by seedlings, derived from varieties originating in the Solomon Islands, Samoa and Malaya, respectively, when growing under strictly comparable conditions.

An experimental nursery was laid down in February 1953. It was located on Ufa Estate where a small group of old Malayan palms were, at the time, being rather severely damaged by *Brontispa*. This was to ensure that there would be good chances of the experimental seedlings being subjected to rapid infestation with the beetle.

Seed nuts, 320 each of Solomon Islands, Samoan and Malayan origin, were planted in a randomised block giving five replicates of each variety in individual plots of 64 palms.

Because the severity of the damage is increased when there is a long interval between the opening of successive fronds, a manurial treatment was incorporated to see if applications of an NPK fertiliser mixture would hasten development and lessen the beetle damage. To accommodate this additional treatment, each main plot was divided to give two sub-plots, each of 32 palms, one without manurial treatment, the other receiving the following fertilisers:—sulphate of ammonia 500 g., superphosphate 500 g., muriate of potash, 300 g.

At the planting distance which was employed, 2 ft. × 2 ft. 6 in., this rate of application is equivalent to a total of approximately 6½ cwt. per acre, a generous rate of manuring.

The lay-out of the plots is illustrated in Pl. IX, fig. 1.

Planting was carried out on 18th and 19th February, after a very wet fortnight (17·34 in. of rain), and subsequent weather was favourable to germination with a further 6 in. of rain before the end of the month.

Germination counts were made at regular intervals, and by the 8th week after planting there were significant differences between the varieties.

Variety	% Germination 14.iv.53 (8 weeks after planting)
Malayan	42·8
Samoan	61·2
Solomon Islands ..	67·8
Standard Error ± ..	1·84

The Malayan nuts were significantly (P = ·01) slower in germinating than either the Samoan or the Solomon Islands varieties.

Eventually, however, the Malayan nearly caught up with the other varieties and there were no significant differences in the final germination percentages, which averaged 84 per cent. over the whole experiment.

Growth was rapid during the first 4–5 months and averaged 5·63 "leaves" per plant when counts were made on 10th July. (The term "leaves" is used here to distinguish this early growth from the typical "fronds" produced after the young seedling stage is passed.)

The Malayan plants were again lagging behind the other varieties:—

Variety	Number of "leaves" per plant 10.vii.53 (20 weeks after planting)
Malayan	5·47
Samoan	5·67
Solomon Islands ..	5·76
Standard Error ± ..	0·073

Although the differences were small, that between Malayan and Solomon Islands, 0·29, proved significant at P = ·05.

The first signs of *Brontispa* damage were observed during the fourth month, and the following figures show the incidence of the attack on each variety at the time of the July leaf counts:—

Variety	Percentage of seedling palms attacked by *Brontispa*
Malayan	27·6
Samoan	10·4
Solomon Islands	11·6

From this stage the severity of the attack increased rapidly. At the same time it became possible to distinguish visually between the Malayan seedlings and those of the other varieties. The former continued to produce undivided seedling "leaves" while both the others commenced the production of "fronds".

Variety	Percentage of plants with pinnate fronds (as opposed to entire "leaves")	
	A 10.vii.53 (aged 20 weeks)	B 1.ix.53 (aged 27 weeks)
Malayan	0	1·7
Samoan	14·2	62·5
Solomon Islands ..	19·8	60·9

The difference in appearance is illustrated in Plate IX, figs. 2 and 3.

The figures set out below indicate the differences between the beetle attack on the three varieties and also the tremendous variation in the level of attack between individual plots within any one variety.

Number of plants attacked by *Brontispa*
(per 100 live palms)
1.ix.53.

Variety \ Block	1	2	3	4	5	Variety means
Malayan	54·0	62·5	40·0	80·0	88·9	65·1
Samoan	54·1	15·5	35·1	57·1	48·2	42·0
Solomon Islands ..	40·0	42·1	60·0	50·0	52·7	48·8
Block means ..	49·1	38·7	45·2	61·9	61·5	52·0

Standard Errors : per plot $\pm$ 14·48
variety means $\pm$ 6·48
block means $\pm$ 8·35

Taking the experiment as a whole, just over half of the palms were attacked by *Brontispa*. Comparing the varieties, only the difference between Malayan and Samoan (23·1%) achieved significance at $P = \cdot 05$ and block differences were as large as those between varieties (Block 4–Block 2, 23·2%).

Neither at this stage nor later did the fertiliser treatment have any effect on the growth of the palms or the amount of damage caused by *Brontispa*.

On 18th November, an attempt was made to differentiate more clearly between the varieties by classifying the extent of the damage suffered by the individual plants.

The youngest expanded frond on each plant was described as undamaged if it bore no *Brontispa* feeding scars at all, fronds with slight or moderate damage were put in a second category, and those on which over one-third of the surface was estimated to have been destroyed were classified as severely damaged.

Variety	Number of plants per 100 showing different degrees of *Brontispa* damage to the youngest open frond, 18.xi.53		
	Undamaged	Slight to moderate damage	Severe damage
Malayan	22	8	70
Samoan	39	18	43
Solomon Islands ..	34	19	47
Mean	32	15	53

While these figures show clearly the greater damage suffered by the Malayan plants, they also show that not one of these three varieties exhibits any strong resistance to *Brontispa* attack. At the time the November observations were made only 17 plants, or just over 2 per cent., remained completely unattacked.

Variety	Percentage of plants not attacked at any time up to 18.xi.53
Malayan	1·7
Samoan	1·7
Solomon Islands	2·9

The experiment was continued until February 1954, when the plants were a year old. By this time every plant showed some *Brontispa* damage and it was estimated that the growth of more than 60 per cent. of them had been seriously retarded.

There is not, in our opinion, any reason for preferring any one of the varieties tested solely on the grounds of its resistance to *Brontispa* attack. Although, as reported by earlier observers, Malayan palms are more susceptible, the successful establishment of Samoan or Solomon Islands palms would be equally impossible in the face of a heavy *Brontispa* attack unless some action were taken to control the beetle.

This conclusion led us to concentrate subsequently on investigating the possibilities of achieving control by the use of insecticides.

Insecticide Experiments.

Information sought in trials.

The object was to try some of the more promising modern insecticides, to see if effective control could be achieved in spite of the failure of earlier methods with older insecticides and the apparent difficulty of application in such a way as to reach the insect in the narrow crevices between the leaflets.

Assuming that an insecticide could be found which would kill the insects, another important point about which information was required was the interval to be left between consecutive applications of insecticide. Owing to reinfestation from surrounding palms, and the fact that fresh fronds are formed and reach a stage vulnerable to attack at more or less frequent, regular intervals, it was obvious that treatment might have to be repeated fairly often. Also, since breeding is not an annual but a continuous process with several generations a year, treatments would have to be kept up throughout the year.

Assuming that the initial treatment is effective against the active stages present at the time, the frequency at which insecticide application must be repeated would appear to depend primarily on the rate of re-invasion. If this is so rapid that the invading adults are themselves numerous enough to cause serious damage, then treatment will have to be repeated often enough to keep the numbers of adults down below the danger level. If it is less rapid, so that damage only becomes serious after the adults have bred and the larvae appear, then a much lower frequency of treatment should be effective, and the life-cycle of the beetle must be taken into account. Lever (1935) and Pagden & Lever (1935) have estimated the total life-cycle from egg to adult as 34·5–41 days, with an average of 38 days. The important thing to know is the incubation period of the eggs, given by Lever as 4–5 days (which has been confirmed by O'Connor (1940) and in the present studies); this means that if the beetles start breeding as soon as they reach the young palms, larvae will probably start appearing after about a week; if there has been any residual effect from insecticide treatment, or if the invasion-rate is slow, it will be considerably longer before the larval population becomes serious.

These considerations were borne in mind when selecting the frequencies of application to be employed. Eventually, applications at the following intervals were tested in one or other of the various experiments—10 days, 2 weeks, 3 weeks, 4 weeks and 6 weeks.

Insecticides used.

DDT, chlordane, BHC and dieldrin were used in a variety of formulations. For the most part these were aqueous sprays, but a kerosene spray and dusts were also tested.

In the Guadalcanal experiments, a succinate wetting agent was employed. A stock solution was prepared by dissolving 100 per cent. succinate wax in acetone at the rate of 1 lb. per pint and this was added to the diluted emulsions at the rate of 2·25 cc. per gallon.

No additional wetting agent was employed with the formulations used in the experiments in the Russell Islands.

Except for the DDT emulsion for Experiment 4, which was prepared at the Long Ashton Research Station, near Bristol, all the insecticides used were the readily available proprietary brands listed below:

- Pespruf 20, a mayonnaise-type emulsion containing 20 per cent. of the p,p′DDT.
- Rulene, a similar emulsion but containing 25 per cent. p,p′DDT.
- Pespruf 4G, a dust containing 2 per cent. p,p′DDT + 0·26 per cent. γ BHC.
- DDT dust, 10 per cent. on talc.
- Eldrinol 25, a miscible oil containing 25 per cent. dieldrin.
- Dieldrin, 15 per cent. emulsion concentrate.
- Octa-Klor, 80 per cent. chlordane emulsion concentrate.

Experimental plots and sites.

Experimental plots for insecticide trials were laid down in two places; on Ufa Estate in the Russell Islands (experiments carried out by A. H. Green), and at

Kukum on Guadalcanal (experiments carried out by E. S. Brown); confirmation of the results of these small-plot trials has been provided by the satisfactory control obtainable by the adoption of the best treatments for more extensive use on recently replanted areas in the Russell Islands (see pp. 269–270).

Experimental plots were all of the same essential type, and comprised groups of seedling palms planted in between mature palms (fig. 1), which were planted at 30 ft. triangular spacing.

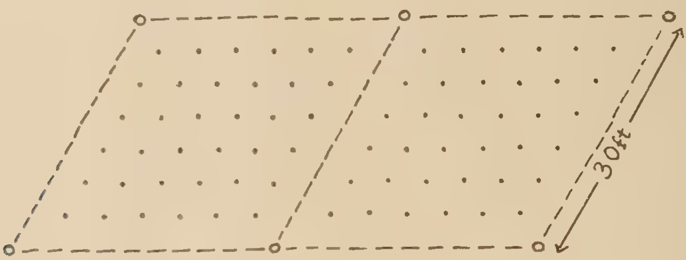

Fig. 1.—Lay-out of experimental plots of young palms (dots) between mature palms (circles) in a plantation.

The number of young palms varied in the different experiments from 16 to 36 per plot whilst the spacing between them varied from 2 ft. × 2 ft. 6 in. to 3 ft. × 6 ft.

In the Ufa experiments, ungerminated nuts were planted (Pl. IX, fig. 1); at Kukum, in order to save time, nuts were planted in which germination had started and there was a shoot up to 1–2 ft. long.

Responsibility for the experiments later described was divided between the authors as follows:—

Russell Islands (A. H. Green): Experiments 1, 2 and 3.
Guadalcanal (E. S. Brown): Experiments 4, 5, 6, 7 and 8.

Assessment of effects of insecticide treatments.

The real importance of treatment, since it is applied to young plants before they have come into production, is the effect it has on the ultimate health of the palm and the age at which it comes into bearing, but since this information would take too long to obtain, other indications had to be used, and the following have been taken into account in our experiments.

(*a*) *Estimates of damage.*—The damage done by *Brontispa* becomes apparent as soon as the frond has unfolded. A convenient way of assessing presence or absence of living *Brontispa* within the last two or three weeks is therefore to examine the youngest opened frond and see if there is any damage. If development and frond formation is slow, the presence of damage may only indicate the earlier presence of living *Brontispa* in more remote periods, even up to six weeks before or possibly more in some cases, but if figures are taken over a whole plot of palms, a swing over from a high to a low percentage of palms showing damage, as the result of successful treatment, becomes detectable within about 2–3 weeks. In most of the experiments on Guadalcanal (Expts. 4–8) an attempt was made to distinguish two degrees of damage, designated "severe" and "light"; severe damage consists of either very heavy damage over not less than half the frond, or of a less marked degree of damage distributed more or less all over the frond; light damage consists of small areas of damage in restricted parts of the frond, often involving not more than two or three leaflets. The distinction is arbitrary, and intermediate conditions are difficult to classify; it is useful, however, in that

it distinguishes conditions which would be expected to affect adversely the health and photosynthetic efficiency of the frond from those which would have little or negligible effect upon it.

(*b*) *Counts of* Brontispa.—These were only undertaken in the experiments at Kukum. The work can be done quite quickly, since many young palms at any one time have no frond in the susceptible stage and therefore no examples of *Brontispa*. Larvae and adults were counted separately; the surprisingly very few pupae were counted in with the larvae; eggs were sometimes noted, but not looked for carefully nor counted. Records were taken for each palm, and totals computed for each plot and each treatment. Counts were made at varying intervals (stated in the description of each experiment), but normally took place immediately before treatments, in order to indicate the degree of persistence of the effect of the previous treatment.

In general, the numbers of *Brontispa* recorded per given number of palms at each count seems small (*e.g.*, Table VI), but it must be remembered that these are distributed only among those palms which have a frond in the susceptible stage at the time the count is made; other palms, if unprotected by treatment, would fall liable to attack at other times.

(*c*) *Leaf counts and height measurements.*—The rate of growth of the palms was estimated by recording the rate of production of new fronds, and by measuring the height of the plants at regular intervals. At each examination the height was measured by drawing the fronds upwards to their full height and measuring from the base of the shoot to the tip of the longest frond (Pl. X, fig. 4). At the same time the youngest open frond was marked by cutting an angular notch out of the terminal margin on one side so that it could be recognised later; at the next count it was then possible to see how many further fronds had opened in the interval.

Although such records were kept both in the Ufa and the Kukum experiments, in the latter the use of non-orthogonal designs precluded statistical treatment of the data, and they have only been analysed for Experiment 2 on Ufa.

Experiment 1. Preliminary testing of insecticides.

The first thing to be determined was which, if any, of the available insecticides would prove lethal to *Brontispa*.

In order to avoid complicating the issue by confusing the efficiency of the insecticides and the efficiency of their application, the preliminary tests were not carried out by treating, in the field, seedlings attacked by *Brontispa*. Instead, pieces of young coconut frond were treated with insecticide and placed in jars. Beetles and larvae were then put into the jars with the treated leaf as their sole food supply.

The first experiment was carried out in August 1953. Four treatments were tested:—

(1) Pespruf 20 diluted 1:100 with water to give a spray containing 0·2 per cent. DDT.
(2) Octa-Klor diluted 1:500 to give a spray containing 0·16 per cent. chlordane.
(3) DDT dust, 10 per cent. on talc.
(4) Pespruf 4G dust.

A randomised block design was used with four replicates of five treatments (4 insecticides and a control). The individual replicates each consisted of a jar containing five adults and five larvae.

The results were encouraging. Amongst the adults, the first deaths occurred in about 36 hours and every beetle in the treated replicates died within six days; there were no casualties in the control replicates where the beetles had untreated leaf on which to feed. Results with the larvae were not quite so conclusive as

there were a number of deaths in the control replicates. However, in the treated replicates only one larva survived at the end of a week and this had pupated.

This preliminary experiment, which showed clearly that DDT and chlordane were both capable of killing *Brontispa*, was followed by a series of similar tests to determine how long the insecticides might remain effective under field conditions. For this purpose a number of young palms were treated with insecticide and pieces of the treated leaf material were removed at intervals of a week for use in new series of jars containing fresh supplies of adult beetles and larvae. These are summarised in Table I.

TABLE I.

Percentage deaths during one week amongst adults and larvae fed on leaf material exposed in the field for various intervals following the application of insecticides.

A. Adults

Treatment	Interval between application of treatment and use of the leaf				Mean
	0	1 week	2 weeks	3 weeks	
Pespruf 20	100	100	100	100	100
Pespruf 4G dust	100	100	100	75	93·8
Octa-Klor	100	90	75	75	85·0
DDT on talc	100	100	100	35	83·8
Mean	100	97·5	93·8	71·2	90·6

Significant differences :	$P = \cdot 05$	$P = \cdot 01$
Margins	10·71	14·32
Body of Table	21·40	28·65

B. Larvae

Treatment	Interval between application of treatment and use of the leaf				Mean
	0	1 week	2 weeks	3 weeks	
Pespruf 20	75	85	90	90	85
Pespruf 4G dust	95	90	95	95	93·8
Octa-Klor	100	85	65	100	87·5
DDT on talc	100	85	85	60	82·5
Mean	92·5	86·2	83·8	86·2	87·2

No statistically significant differences.

Considering first the figures relating to adults, it will be seen from the Table that only Pespruf 20 remained completely effective for the full period. Octa-Klor was significantly less effective in the third and fourth weeks after application (leaf kept for 2 or 3 weeks before being used) whilst the dusts, Pespruf 4G and DDT on talc, also showed signs of diminished efficiency in the fourth week. Averaging the figures for the four periods, Pespruf 20 proved significantly better than Octa-Klor or DDT on talc.

The data for the larvae were much more variable and there were no significant differences between the insecticides. However, they all achieved a large measure of control with an average kill of 87·2 per cent.

In the parallel series of control tests, losses over all periods averaged 18·8 per cent. amongst the adults and 25 per cent. amongst the larvae.

The results of this experiment were considered to justify a more extensive trial under field conditions.

Experiment 2. Field trial with DDT and chlordane.

Although Experiment 1 had shown that either sprays or dusts could be used to kill *Brontispa*, it was considered that spraying offered better chances for the insecticide to penetrate between the leaflets of the unexpanded fronds and so protect the vulnerable leaf surfaces. Pespruf 20 and Octa-Klor were therefore selected for a further trial under field conditions.

A nursery of 960 Malayan seedling palms had been planted in July 1953 on a site adjacent to the variety trial. This too was laid out beneath heavily infested mature palms in an arrangement which gave 32 plots, each of 30 seedlings.

For nearly three months there was no sign of *Brontispa* attack; but after four months every one of the 960 seedlings showed some signs of *Brontispa* damage. The nursery was thus an ideal site for the field testing of the two insecticides.

A 4 × 2 × 2 factorial design was used to test 4 rates and two frequencies of each of the two insecticides.

A. Rates of application.—As the spraying equipment available did not permit the accurate control of the volume of spray applied and the spray lances were fitted with twin nozzles designed for the application of high volumes of solution per acre, it was necessary to obtain the different rates of application by using different concentrations of insecticide in the same total volume of spray for all plots. To ensure thorough coverage it was found necessary to apply the equivalent of 100 gallons of spray per acre.

Concentration of insecticide in aqueous sprays.

Rate	Pespruf 20 (% DDT)	Octa-Klor (% chlordane)
a_0 control ..	0	0
a_1 low	0·1	0·08
a_2 medium ..	0·2	0·16
a_3 high	0·3	0·24

In the absence of any previous experience, the choice of the different concentrations of DDT was somewhat haphazard but, having selected these rates for DDT, the rates for chlordane were calculated so as to equalise the cost of the two insecticides.

B. Frequencies of application.—Since, in Experiment 1, it was shown that the efficiency of the insecticides declined in the fourth week, the lower frequency was selected as three weeks. This was compared with applications every 10 days, the object being to see if the more frequent spraying would give better protection by ensuring that every frond was treated within a few days of reaching the susceptible stage.

b_0 = spraying every 10 days
b_1 = spraying every 3 weeks

C. Types of insecticide.—These, as already stated, were DDT in the form of Pespruf 20 and chlordane as Octa-Klor.

c_0 = DDT
c_1 = chlordane

The 16 combinations of the a, b and c treatments were divided into two sets of eight by confounding the interaction A ′ ′ ′ BC and the sets of eight were allocated at random within the four blocks.

It will be noticed that the design involves a number of dummy treatments since any of the four combinations of b and c with a_0 is in fact an unsprayed or control plot so that there are two control plots in each block. This was considered an advantage on account of the erratic variations in severity of attack which had been observed from block to block on the variety trial.

Treatment commenced on 17th November 1953, and applications were continued for 15 months, *i.e.*, until the end of February 1955, when the experiment was discontinued.

It very soon became apparent that all the treatments were exercising some control over *Brontispa*.

On 3rd April 1954 the following figures were recorded:

(a) the total number of fronds per palm,

(b) The number of fronds per palm badly damaged by *Brontispa*.

The general mean for numbers of fronds per palm was 6·56 and there were no significant differences as a result of the treatments.

For arriving at figures for numbers of "badly damaged" fronds, any frond was so classified if it appeared on a visual assessment to have more than a third of its surface destroyed by *Brontispa*.

The severity of the *Brontispa* damage was then assessed by expressing, for each plot, the number of badly damaged fronds as a percentage of the total number of fronds on the 30 palms in the plot. The results are summarised in Table II.

TABLE II.

Assessment of *Brontispa* damage on palms sprayed with DDT or chlordane. Numbers of badly damaged fronds as a percentage of the total number of fronds, 3rd April 1954.

A	Rates of application (averaged over frequencies and types of insecticide)	
		%
	Control	39·6
	Low rate	3·5
	Medium rate	3·4
	High rate	1·8
B	Frequency of application (averaged over 3 rates and types)	
		%
	10 days	1·5
	3 weeks	4·2
C	Types of insecticide (averaged over 3 rates and 2 frequencies)	
		%
	DDT	3·0
	Chlordane	2·8

On the untreated control plots nearly 40 per cent. of all fronds produced had been badly damaged. In spite of this clear evidence of continuing heavy *Brontispa* attack on the area, not one of the treated plots showed a high percentage of serious damage.

Although damage on the high-rate plots at 1·8 per cent. was less than on the low-rate plots, 3·5 per cent., this difference was not statistically significant and even the low rate clearly gave the palms a large measure of protection.

There was no appreciable difference between DDT and chlordane, but spraying with either insecticide every 10 days (1·5% damage) gave better protection than the 3-weekly treatments (4·2% damage).

One surprising feature of the treatments was that many of the young fronds were opening with no signs at all of *Brontispa* feeding scars, thus showing that in spite of the far from ideal equipment, which produced a low-pressure spray of large droplet size, the insecticides were penetrating between the leaflets of any frond that had expanded sufficiently to permit the entry of the beetles.

The virtual elimination of serious damage by all the treatments made it necessary to use a more stringent test for future comparisons.

When damage estimates were made in May, June and July, only the youngest open frond on each palm was examined, and it was recorded as attacked if it showed any signs at all of *Brontispa* feeding scars. This system obviously could not credit any treatment with effecting 100 per cent. control because even if all immigrant adult beetles were killed some of them would do a certain amount of feeding before they succumbed. The method also under-estimated the difference between the control plots and any of the treated plots. In spite of these drawbacks the method served to reveal significant differences between the various rates, frequencies and types of insecticide.

TABLE III.

Percentage of palms showing *Brontispa* feeding scars on the youngest open frond when examined on the dates indicated.

Treatment		18th May	18th June	29th July
A		%	%	%
Rate	Control	100	97	99
	Low rate	36	40	46
(240 palms per treatment)	Medium rate	21	35	37
	High rate	20	25	31
B				
Frequency	10 days	20	25	30
(360 palms per treatment)	3 weeks	31	41	46
C				
Insecticide	DDT	19	20	30
(360 palms per treatment)	Chlordane	32	46	46

The increase in the average percentage of attacked palms with the passing of time (see Table III), was attributed to the presence of increasing numbers of beetles leaving the devastated control plots in search of new food supplies. The percentage figures for attacked palms averaged over all treated plots were:—

18th May	18th June	29th July
26%	33%	38%

In spite of this increase, even in July there were no treated palms that would have been classified as severely damaged by the standards used for the first estimates carried out in April.

In May, both the medium and high rates were more effective than the low rate ($P = \cdot 01$), but in June the difference of 15 per cent. between the high and low rates failed to achieve statistical significance.

On every occasion DDT gave better results than chlordane ($P = \cdot 01$) and spraying every 10 days was always better than every three weeks ($P = \cdot 05$ in May and June; $P = \cdot 01$ in July).

At this stage the young palms had to be thinned out by removing the second and fourth row from each plot, thus leaving 18 palms per plot instead of the original 30.

One consequence of this reduction in plant number was that the treatment differences indicated by the August, September and October estimates of damage failed to achieve statistical significance.

An attempt was made to increase the sensitivity of the estimates by introducing a severity rating; 0, 1, 2 or 3 points were scored by undamaged, very slightly damaged, moderately damaged, and severely damaged fronds, respectively.

Thus a plot on which the youngest frond of every palm was severely damaged would score 54 points. The expression of the actual scores recorded as a percentage of this maximum afforded a convenient basis for comparing the treatment effects. The following figures illustrate the position at the end of February 1955.

Rate	Control 48%	Low rate 12%	Medium rate 8%	High rate 7%
Frequency	10 days 6%		3 weeks 12%	
Insecticide	DDT 8%		Chlordane 10%	

The difference between any of the treatments and the controls was highly significant ($P = \cdot 001$), but the only significant difference revealed by comparisons amongst the treated plots was the superiority of 10-day over 3-weekly applications ($P = \cdot 05$). The low rate of application every 10 days (score 8%) was as good as the high rate every 3 weeks (score 10%) and even the most economical treatment, the low rate every 3 weeks, which scored 15 per cent., afforded the palms adequate protection for all practical purposes as there were no cases of severe damage on any of the treated plots.

TABLE IV.

The effect of DDT- and chlordane-based insecticides on the growth of young palms attacked by *Brontispa*.

Treatments		Mean number of fronds per palm		Mean height per palm (ft.)		Mean weight per palm (lb.)	
General Mean Standard Error ±		6·47 0·070		5·64 0·083		4·28 0·052	
A Rate			%		%		%
	Control	6·23	100	4·87	100	3·41	100
	Low rate	6·76	108*	6·16	126***	5·08	149***
	Medium rate	6·58	106	5·72	117**	4·21	123*
	High rate	6·33	102	5·81	119***	4·42	130**
B Frequency	10 days	6·35	100	5·89	100	4·47	100
	3 weeks	6·76	106*	5·91	100	4·67	105
C Insecticide	DDT	6·42	100	5·72	100	4·45	100
	Chlordane	6·68	104	6·07	106	4·70	106

Measurements recorded in February 1955, palms aged 19 months.

(*, **, and *** denote statistical significance at $P = \cdot 05$, $\cdot 01$ and $\cdot 001$, respectively.)

After the final damage estimates were completed, frond counts and height measurements were made, and all the palms were cut off at ground level and the tops weighed to see what effect the treatments had had on their growth. The results are summarised in Table IV.

The most obvious feature of the data is that although all the treatments had led to better growth than on the unsprayed plots, comparisons between the treatments reveal effects in all cases opposite to what one would expect from a consideration of the *Brontispa* damage estimates.

Thus, although the high rate gave better control of *Brontispa* than the medium or low rates (Table III), plants receiving the low rate of application made the best growth and although all three rates significantly increased the height and weight of the palms, only the low rate also increased the number of fronds. Spraying every 10 days gave better control of the beetle, but palms sprayed every 3 weeks made the better growth. Palms sprayed with DDT suffered less beetle damage (Table III) but made poorer growth (Table IV) than those treated with chlordane.

Further analysis of these contradictory results indicated that the DDT formulation (Pespruf 20) has slight phytotoxic properties.

A complete breakdown of the data to permit calculation of the interactions between rates, frequencies and types of insecticide gave individual figures based on only 36 palms (sums of 2 plots) and the results were inconclusive.

However, by averaging over the three rates, it was shown that there was a significant frequency × insecticide interaction in the data for numbers of fronds ($P = \cdot 05$), and the height measurements and plant weights also agreed in indicating that the poorest growth was made by plots receiving applications of Pespruf 20 every 10 days.

TABLE V.

Growth measurements on young palms receiving different frequencies of application of DDT and chlordane, averaged over 3 rates of application and expressed as a percentage of the corresponding data from untreated control plots.

Insecticide	Frequency	No. of fronds	Height (ft.)	Plant weight (lb.)
DDT	10 days	97	116	124
	3 weeks	109	119	137
Chlordane ..	10 days	107	126	138
	3 weeks	107	124	137

It will be seen from Table V that palms which were treated with DDT every 10 days actually produced fewer fronds than the palms on the control plots.

We do not attach much importance to these indications of phytotoxicity. The use of unsuitable spraying equipment in this experiment necessitated the application of about 100 cc. of spray per palm to ensure thorough coverage. In subsequent experiments, better equipment permitted as good results from the point of view of *Brontispa* control with only 10–20 per cent. of the volume of spray and the risk of phytotoxicity at these concentrations may almost certainly be ignored.

Experiment 3. A comparison between DDT and dieldrin at different rates and frequencies.

A new nursery of 768 Malayan seed nuts was planted adjacent to Experiment 2 on 5th May 1954. This comprised 24 plots, each of 32 seedlings, and was used

to compare dieldrin, so far untried in these experiments, with the 1·5 per cent. Pespruf 20 (0·3% DDT) treatment which gave the best results, from the point of view of *Brontispa* control, of the treatments already being tested in Experiment 2.

The 24 plots permitted fourfold replication of the following six treatments in a pseudofactorial arrangement:—

A (1) DDT (0·3%) every 10 days.
(2) Dieldrin (0·1%) every 10 days.
(3) Dieldrin (0·1%) every 3 weeks.

B (1) High-volume spraying.
(2) Low-volume spraying.

A. Rate and frequency of application.—The dieldrin was used at 0·1 per cent. in order to equalise the cost with that of the 0·3 per cent. DDT. It was prepared by using the standard 15 per cent. emulsion concentrate at a dilution of 1 part of concentrate in 130 parts of water. Although the DDT treatment was used only at the 10-day frequency, it was thought worth while to test dieldrin also at the 3-week interval.

B. High- and low-volume spraying.—The knapsack sprayers used in Experiment 2 were obviously wasteful and inefficient, and it was clear that a big saving might be made if satisfactory control could be achieved by low-volume applications using a different type of sprayer. The knapsack sprayers were, therefore, compared with Rega atomisers, small hand sprayers of 1-pint (568 cc.) capacity, designed to deliver a very fine mist of insecticide. Using these atomisers, it was found that the target area, that is, the young frond in the centre of the palm that was just beginning to unfurl, could be thoroughly wetted with as little as 6 cc. of insecticide, and 200 cc. were used per plot of 32 palms. The high-volume applications were at ten times this amount, that is, 2 litres per plot.

Unfortunately, the beetle damage on these plots was not severe and when treatment was commenced on 13th September, 19 weeks after planting, only 130 of the 768 palms were attacked.

As soon as spraying commenced, the *Brontispa* damage on all plots fell to negligible proportions. In November, only nine palms showed any damage to the youngest open frond. In February 1955, spraying was discontinued in an attempt to let the *Brontispa* population build up, but by June only 92 palms, or 12 per cent. of the total, were noticeably attacked, and it was obvious that there was no possibility of differentiating between the efficiency of the various treatments by a resumption of spraying. The experiment was therefore abandoned. The only conclusion to be drawn from it was that against a light attack by *Brontispa* all the treatments were completely effective and it was clearly worth while persisting with further testing of low-volume spraying under more favourable circumstances.

Experiment 4. Trial with DDT (Long Ashton formulation), chlordane and dieldrin.

This experiment, the first carried out at Kukum on Guadalcanal, was designed to compare the effects of DDT at 0·25 per cent. and 0·025 per cent., dieldrin at 0·15 per cent., and chlordane at 0·16 per cent., and thus included all three of the insecticides tested in previous trials on Ufa. All these treatments were applied as aqueous emulsions, and a succinate wetting agent was added. At the outset, certain plots also were sprayed with the DDT formulation in odourless kerosene, with control plots sprayed with odourless kerosene alone; but since these treatments resulted in the rapid death of the palms, due probably to the spray being too coarse, they were discontinued. The original number of plots was 24 (12 of them containing 16 palms each and 12 containing 36), but this was reduced, by

the elimination of the kerosene-sprayed plots, to 19, which were distributed between the various treatments as follows (F = under fortnightly treatment, and M = under monthly treatment).

Treatments	Small plots		Large plots		Total plots		Total palms	
	F	M	F	M	F	M	F	M
Dieldrin (0·15%)	1	1	1	1	2	2	52	52
DDT (0·25%)	1	–	1	1	2	1	52	36
Chlordane (0·16%)	1	–	1	1	2	1	52	36
DDT (0·025%)	1	–	1	1	2	1	52	36
All treated plots	4	1	4	4	8	5	208	160
Control (untreated)	3		3		6		156	

As far as numbers of plots and palms are concerned, therefore, all treatments are similar except dieldrin, which was applied to one extra plot of 16 palms.

The plots were in a single line alongside the Honiara–Kukum road, the 16-palm plots in one block separated from the 36-palm plots by a distance of about ¼ mile. All were planted in triangular formation under mature palms infested by *Brontispa*, as in Experiments 2 and 3. The nuts were the local Solomon Islands type.

The plots were laid down in October 1955. The young palms were allowed to grow and become infested by *Brontispa* without interference for four months, until early March 1956. During this period, regular counts of *Brontispa* were made every fortnight in all plots, and the population had by then acquired some degree of stability in most of the plots (Table VI). To indicate the build-up in numbers, the total numbers of adults and larvae combined in all plots (as distinct from the numbers per 100 palms shown in Table VI) were for the 9 consecutive pre-treatment counts: 58, 116, 160, 161, 179, 274, 371, 427, 351. Similar combined counts for the control plots, which were unaffected by any treatment, were as follows for the whole duration of the experiment: 2, 5, 27, 42, 49, 70, 68, 87, 97, 143, 121, 113, 154, 130, 159, 185, 246, 80, 129, 196, 138 (the first two figures, 2, 5, are for two earlier counts unrepresented in Table VI); it will be seen that the population, although fluctuating, had reached a more or less average maximum level by the time treatments started.

Insecticides were applied by means of a stirrup pump connected by a hose to a 2-ft. lance with a trigger tap; the nozzle was of the swirl-plate type with a disc having an aperture of 0·039 ($\frac{5}{128}$) in., and was fitted at an angle of 45° to the lance; this made it easy to direct a jet of spray downwards into the centre of the palm (Pl. X, fig. 3), and the trigger tap enabled the operator to apply the small amount of spray necessary for each palm with a minimum of wastage. The volume of diluted spray used with this equipment averaged slightly under one pint (568 cc.) per plot of 36 palms. This is equivalent to about 16 cc. per palm and is more nearly comparable to the low volume treatments of Experiment 3 than the high volume used in Experiment 2.

The first treatment (for plots under both monthly and fortnightly treatment) was applied on 6th March 1956. Thereafter, treatments were applied at regular fortnightly or monthly intervals as the case might be, until September 1956. *Brontispa* counts were continued at fortnightly intervals until 29th May, and then at monthly intervals until 18th September (Table VI); they were always made just before a treatment, so that they indicated the effectiveness of treatments right up to the end of the interval between the treatments and would thus show up any reinfestation which had taken place.

TABLE VI.

Brontispa counts in plot trial (Experiment 4) at Kukum with dieldrin, chlordane and DDT. Numbers of adults and larvae are recorded separately and combined, at regular intervals, both during the build-up in numbers before the commencement of spraying, and during the period after spraying had started. The very few pupae recorded are included with the larvae.

Treatments	No. of palms	Numbers of *Brontispa* revealed by counts on dates shown; each figure represents the number per 100 palms, calculated from the actual counts																											
		1.xi.55			15.xi.55			3.xii.55			16.xii.55			3.i.56			16.i.56			31.i.56			14.ii.56			29.ii.56			6.iii.56
		Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	
A Fortnightly																													First Application of Treatment
(1) Dieldrin (0·15%)	52	4	2	6	4	21	25	13	25	38	8	15	23	2	12	14	6	8	14	21	6	27	31	8	39	42	0	42	
(2) DDT (0·25%)	52	4	4	8	21	8	29	15	19	34	13	13	26	31	25	56	27	44	71	60	69	129	71	31	102	67	54	121	
(3) Chlordane (0·16%)	52	10	25	35	2	12	14	2	13	15	10	12	22	13	2	15	37	21	58	23	33	56	69	13	82	71	25	96	
(4) DDT (0·025%)	52	0	0	0	2	4	6	4	50	54	12	23	35	15	25	40	44	44	88	75	90	165	77	67	144	50	13	63	
B Monthly																													
(1) Dieldrin (0·15%)	52	0	0	0	19	37	56	12	13	25	21	17	38	38	12	50	44	10	54	46	13	59	63	15	78	35	0	35	
(2) DDT (0·25%)	36	0	0	0	6	0	6	3	3	6	0	0	0	8	0	8	25	33	58	17	44	61	28	50	78	78	6	84	
(3) Chlordane (0·16%)	36	0	0	0	0	8	8	8	50	58	14	19	33	28	3	31	3	3	6	22	6	28	22	0	22	22	0	22	
(4) DDT (0·025%)	36	6	11	17	3	0	3	0	3	3	11	0	11	14	0	14	31	14	45	36	6	42	44	0	44	17	0	17	
C Control Untreated	156	6	11	17	7	20	27	15	17	32	13	32	45	22	22	44	30	26	56	43	19	62	66	26	92	56	22	78	

Treatments	No. of palms	Numbers of *Brontispa* revealed by counts on dates shown ; each figure represents the number per 100 palms, calculated from the actual counts																													
		20.iii.56			3.iv.56			17.iv.56			1.v.56			15.v.56			29.v.56			26.vi.56			24.vii.56			21.viii.56			18.ix.56		
		Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total
A Fortnightly																															
(1) Dieldrin (0·15%)	52	0	0	0	10	0	10	2	0	2	4	0	4	2	0	2	2	0	2	2	0	2	0	0	0	0	0	0	0	0	0
(2) DDT (0·25%)	52	6	0	6	15	0	15	27	0	27	17	2	19	0	0	0	2	2	4	13	0	13	0	0	0	0	0	0	4	8	12
(3) Chlordane (0·16%)	52	6	0	6	17	0	17	13	0	13	6	15	21	2	0	2	12	0	12	8	0	8	4	4	8	10	0	10	2	0	2
(4) DDT (0·025%)	52	42	2	44	50	4	54	28	40	68	36	46	82	31	46	77	10	8	18	27	2	29	10	2	12	17	8	25	4	13	17
B Monthly																															
(1) Dieldrin (0·15%)	52	2	0	2	12	0	12	12	0	12	8	8	16	4	0	4	15	0	15	0	0	0	4	0	4	0	0	0	2	0	2
(2) DDT (0·25%)	36	3	0	3	33	8	41	11	0	11	19	14	33	6	0	6	19	0	19	17	0	17	3	0	3	11	11	22	14	0	14
(3) Chlordane (0·16%)	36	3	0	3	25	0	25	33	0	33	17	0	17	3	0	3	33	61	94	8	0	8	8	0	8	8	0	8	0	0	0
(4) DDT (0·025%)	36	14	0	14	61	0	61	72	17	89	44	0	44	36	14	50	14	0	14	19	3	22	8	39	47	3	0	3	6	0	6
C Control Untreated	156	44	29	73	74	24	98	57	27	84	47	55	102	61	58	119	74	83	157	40	12	52	37	46	83	58	68	126	24	64	88

All the counts, expressed as numbers of *Brontispa* per 100 palms, are given in Table VI. Adults and larvae are shown separately, as well as combined figures for both stages. The immediate effect of treatment on numbers is very evident. For plots treated with 0·15 per cent. dieldrin, 0·25 per cent. DDT and 0·16 per cent. chlordane, there is considerable reduction in numbers of adults in all subsequent counts, and almost complete disappearance of larvae, showing that breeding has been practically eliminated. The lower percentage of DDT, on the other hand, produced much less reduction in adults, and larvae continued to occur in some numbers.

Further analysis of the *Brontispa* counts is presented in Table VII. Here, average figures are given for all counts after treatment began, for comparison with the last five counts before the first treatment (*i.e.*, for the period during which the population showed a measure of stability).

TABLE VII.

Brontispa counts in comparative trial (Experiment 4) with dieldrin, chlordane and DDT, showing average numbers of living *Brontispa* before and after treatment.

Treatments	Average numbers of *Brontispa* per 100 palms at each count					
	For last 5 counts before first treatment			For first 10 counts after first treatment		
	Adults	Larvae	Total	Adults	Larvae	Total
A Fortnightly						
(1) Dieldrin (0·15%)	20·4	6·8	27·2	2·2	0	2·2
(2) DDT (0·25%) ..	51·2	44·6	95·8	8·4	1·2	9·6
(3) Chlordane (0·16%)	42·6	18·8	61·4	8·0	1·9	9·9
(4) DDT (0·025%) ..	52·2	47·8	100·0	25·5	17·1	42·6
B Monthly						
(1) Dieldrin (0·15%)	45·2	10·0	55·2	5·9	0·8	6·7
(2) DDT (0·25%) ..	31·2	26·6	57·8	13·6	3·3	16·9
(3) Chlordane (0·16%)	19·4	2·4	21·8	13·8	6·1	19·9
(4) DDT (0·025%) ..	28·4	4·0	32·4	27·7	7·3	35·0
C Control						
Untreated ..	43·4	23·0	66·4	51·6	46·6	98·2

The pre-treatment data reveal that the initial degree of infestation varied greatly from plot to plot. For example, the total *Brontispa* population on the fortnightly DDT plots was more than 3·5 times as numerous as that on the plots subsequently receiving fortnightly applications of dieldrin. It is improbable that these pre-treatment figures reflected accurately the invasion pressure to which the plots were subjected during the whole of the subsequent treatment period. However, it seemed desirable to make some correction for this lack of uniformity and since statistical treatment of the data (*e.g.*, by co-variance analysis) was precluded by the design of the experiment, it was decided to calculate the percentage control of the beetle population achieved by each treatment from the expression:—

$$\%\ \text{Control} = \frac{(\text{pre-treatment} - \text{post-treatment})}{\text{pre-treatment}} \times 100$$

and to use the resulting figures as the basis for comparisons between the various treatments.

These figures, with an indication of the initial severity of attack in each treatment (maximum score = 10), are set out in Table VIII.

TABLE VIII.

Percentage control of *Brontispa* achieved by insecticide treatments, calculated from pre-treatment and post-treatment population counts of adults and larvae.

Treatment	Severity of attack	Percentage control		
		Adults	Larvae	Total
A Fortnightly		%	%	%
(1) Dieldrin (0·15%) ..	3	89	100	92
(2) DDT (0·25%) ..	10	84	97	90
(3) Chlordane (0·16%) ..	6	81	90	84
Mean 1 — 3 ..	6	84	96	88
(4) DDT (0·025%) ..	10	51	64	57
B Monthly				
(1) Dieldrin (0·15%).. ..	6	87	92	88
(2) DDT (0·25%) ..	6	56	87	71
(3) Chlordane (0·16%) ..	2	29	— 150	9
Mean 1 — 3 ..	5	65	74	68
(4) DDT (0·025%) ..	3	2	— 82	— 8
C Control				
Untreated	7	— 19	— 103	— 48

Perhaps the best indication of the relative value of the treatments is their control of the larvae, for this indicates the extent to which breeding is being suppressed and therefore the degree to which populations are prevented from becoming established.

Considering first the results of the fortnightly applications, there was clearly nothing to choose between dieldrin and DDT (0·25%); a complete control of a light attack by dieldrin could not be considered superior to the 97 per cent. control of a very heavy attack by DDT. Both dieldrin and DDT (0·25%) were rather more effective than chlordane, but all three insecticides, applied fortnightly, gave very satisfactory results. Even the DDT (0·025%) gave some protection at this frequency, though it was obviously not comparable with the other three treatments and was omitted when calculating the mean values for comparing fortnightly and monthly treatments.

The results of the monthly treatments show a clear difference between the insecticides that was not apparent with the more frequent applications. Both dieldrin and DDT (0·25%) continued to give good control of the larvae but dieldrin showed itself superior in dealing with immigrant adults, 87 per cent. control, as against 56 per cent. for DDT and only 29 per cent. for chlordane. At monthly intervals the chlordane apparently ceased to exercise any control at all over the larvae (*cf.* Experiment 1).

On the control plots the population of both adults and larvae continued to increase throughout the period.

Records of *Brontispa* damage to the youngest open frond were made on four occasions at intervals of two months, the first being at about the time of the first insecticide treatment. Each palm was classified as severely damaged,

lightly damaged, or without any damage, and for each treatment the percentage of palms in each category was calculated at each examination (Table IX). The reduction of severely damaged palms in all treated plots is very evident.

Dieldrin, even at the monthly frequency, completely eliminated severe damage as the experiment progressed (see Table IX) so that the estimates tend to confirm its superior residual effects, already indicated by the beetle population counts (Table VII). Severe damage was never completely eliminated on the 0·25 per cent. DDT plots but it has to be remembered that the plots treated fortnightly with this insecticide were subjected to particularly heavy attack (Table VIII). In spite of this, both frequencies reduced the amount of severe damage to an insignificant level, and there was never more than one severely damaged palm in either treatment when the later estimates were carried out.

Chlordane prevented severe damage when applied fortnightly but the reappearance of severe damage on the monthly treated plots after six months may reflect the failure of this treatment to prevent breeding.

The figures for light damage are probably indicative of the severity of attack as well as of the efficiency of the treatments. Since none of the insecticides has an immediate knockdown action, any palm visited by a large number of adults will show some damage even though the beetles subsequently die. This may be illustrated by a comparison between the pre- and post-treatment beetle counts (Table VIII) and damage estimates for the fortnightly and monthly chlordane and DDT (0·25% and 0·025%) treatments (Table IX). In all three instances the initial attack was more severe on the fortnightly treated plots and despite the obviously greater efficiency of the fortnightly applications (beetle population counts) light damage throughout the experiment continued to be greater on the fortnightly than on the monthly treated plots.

Records were also made of the heights of the palms and the numbers of new fronds produced. Unfortunately, growth on the different plots was very variable owing to inequalities in the sites (*e.g.*, two plots were found to have been planted in shallow soil covering an old roadway), and the growth measurements failed to indicate any consistent differences as a result of the insecticide treatments. However, all plots, except the two just referred to, on which the beetle was successfully controlled showed much more vigorous development than any of the untreated plots and there were no obvious indications of phytotoxicity.

In view of the apparent superiority of dieldrin over either DDT or chlordane (in the formulations used in this experiment), which was attributed to its more lasting residual effect, it was selected for use in further trials at Kukum which are described in the following pages.

Experiment 5. Plot trial with dieldrin, applied at fortnightly and monthly intervals.

Selecting 0·15 per cent. dieldrin as the most effective of the treatments used in the preceding experiment, a further trial was carried out with this alone. The method was the same as before. Eight plots, each of 36 palms, were used. Four were treated, two of them at fortnightly and two at monthly intervals; the

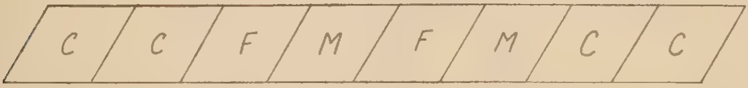

Fig. 2.—Lay-out of plots for Experiment 5. C, control plots (unsprayed); F, M, plots sprayed with 0·15% dieldrin at fortnightly and monthly intervals, respectively.

TABLE IX.

Brontispa spraying trial (Experiment 4) at Kukum with dieldrin, chlordane and DDT, showing extent of *Brontispa* damage to the youngest opened frond at the time of the first spray treatment, and at intervals of two months afterwards.

Treatments	No. of palms	Numbers of palms in different damage categories on the dates indicated, expressed as percentage of all palms under the treatment and spraying frequency specified											
		15–16.iii.56			15–18.v.56			16.vii.56			17.ix.56		
		Severe damage	Light damage	No damage	Severe damage	Light damage	No damage	Severe damage	Light damage	No damage	Severe damage	Light damage	No damage
A Fortnightly													
(1) Dieldrin (0·15%)	52	8	38	54	0	8	92	0	0	100	0	2	98
(2) DDT (0·25%)	52	27	60	13	2	50	48	2	29	69	2	33	65
(3) Chlordane (0·16%)	52	13	52	35	0	38	62	0	36	64	0	36	64
Mean 1–3	(156)	16	50	34	1	32	67	1	22	77	1	24	75
(4) DDT (0·025%)	52	35	46	19	12	48	40	0	60	40	6	52	42
B Monthly													
(1) Dieldrin (0·15%)	52	27	35	38	4	21	75	0	21	79	0	21	79
(2) DDT (0·25%)	36	17	44	39	3	44	53	3	28	69	3	25	72
(3) Chlordane (0·16%)	36	14	31	55	3	31	66	0	8	92	3	11	86
Mean 1–3	(124)	20	36	44	3	31	66	1	19	80	2	19	79
(4) DDT (0·025%)	36	20	44	36	22	42	36	0	36	64	0	19	81
C Control Untreated	156	55	21	24	31	36	33	31	33	36	37	32	31

remaining four were left untreated as controls. The plots were in a single row; the four central ones were sprayed, and two at each end were left as controls (fig. 2). The object of this arrangement was to avoid as far as possible any "proximity" effect of spraying upon the control plots which might result if they were alternated with treated plots. The plots were situated under mature palms which were mostly infested, so that all plots were approximately equally exposed to attack. Spraying of the treated plots was started immediately after planting, without waiting for a population of *Brontispa* to build up.

Results were assessed by counting living *Brontispa* in all plots at intervals. The first count was made two days after the first spraying; later counts were made at fortnightly intervals for six weeks, and then at monthly intervals for the next four months; a final count was made after a further lapse of three months, and the experiment was then discontinued. All counts except the first were made immediately before a spray treatment, so that any build-up in numbers during intervals between spraying could be assessed.

TABLE X.

Numbers of live *Brontispa* recorded between 20.iv.56 and 10.xii.56, totalled over 9 counts (Experiment 5).

Treatment	Adults	Larvae	Total
Dieldrin (0·15%) fortnightly	1	0	1
Dieldrin (0·15%) monthly ..	0	0	0
Control — no spraying ..	197	191	388

The number of palms involved was 72 for each treatment, and 144 for the controls.

The results, shown in Table X, were highly conclusive. Whereas in the control plots a total of 388 living *Brontispa* were counted, including approximately equal numbers of adults and larvae, in the treated plots only a single living adult was recorded, and no larvae at all. The single adult was in one of the plots under fortnightly treatment, and was doubtless one which had flown in shortly before the count was made.

The total numbers of living and dead specimens recorded at all counts for treated and untreated palms (the number of palms being 144 in each case) were as follows:—

	Treated palms	Controls
Living	1	388
Dead	21	1

It is evident that against the level of attack to which these young palms were subjected both the fortnightly and monthly treatments were completely effective and it might have been possible to extend the interval between treatments further, perhaps to six weeks, without serious damage.

The quantity of spray used was extremely small, averaging $\frac{7}{8}$ pint (497 cc.) of 0·15 per cent. dieldrin per plot of 36 palms, or approximately $\frac{1}{2}$ oz. (14·2 cc.) per plant.

Experiment 6. Long-interval spraying trial.

In order to find whether, in favourable circumstances at least, the interval between treatments could be safely extended beyond those left in other experiments, a small coconut nursery of 93 palms at Kukum was selected for treatment.

The palms were about one year old, planted close together (12–15 in. apart) in three double rows, and were in a rather sheltered position; the nearest native coconut palms infested by *Brontispa* were some 200 yd. distant. Infestation of the young palms in the nursery was very high, and the youngest open frond was

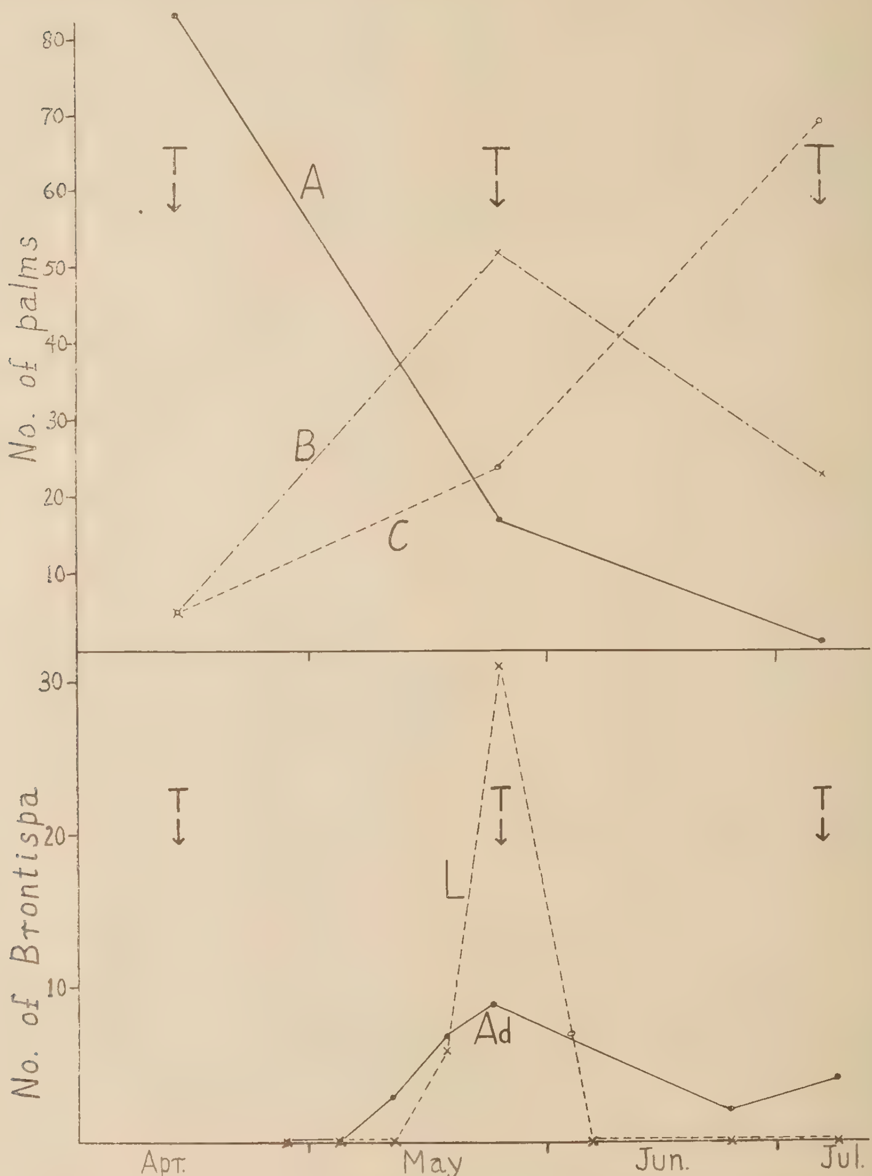

Fig. 3.—Long-interval spraying trial with dieldrin (Experiment 6). Upper graph: numbers of palms showing (A) severe, (B) light, and (C) no damage on dates shown. Lower graph: total number of *Brontispa* on dates shown: Ad, adults; L, larvae; T, dates of spray treatments.

severely damaged in no less than 83 of them (89·2%) at the start of the experiment.

All the palms were sprayed with a stirrup pump with 0·15 per cent. dieldrin at six-weekly intervals, on 13th April, 25th May and 6th July; on the same dates the youngest open frond was examined for *Brontispa* damage. At the second spraying the number of palms with severely damaged fronds had fallen from 83 to 17, and at the third to only 1 (1·08%) (see fig. 3); the number without any damage had risen from 5 to 24 at the second spraying, and to 69 at the third; there were then still 23 palms with slight damage, but since in these the damage was not sufficient to affect the health of the palms, we can say that practically 100 per cent. protection had been achieved by spraying at six-weekly intervals. Probably this is about the minimum frequency that will give satisfactory control where there is constant re-invasion from mature palms. Vigorous young palms produce a new frond about every six weeks and it is clearly desirable to spray each emergent frond at least once during the period when it is susceptible to attack. As in the previous experiment, each palm required only about ½ oz. (14·2 cc.) of 0·15 per cent. dieldrin spray at each treatment so that protection was obtained at very low cost.

Counts of *Brontispa* were made at irregular intervals during the period (fig. 3). The build-up in numbers was very slow. Five weeks after the first spraying there were only 7 adults and 6 larvae altogether, and by the time of the second spraying, there were nine adults and 31 larvae, averaging less than one individual of *Brontispa* to every two palms. Between the second and third treatments build-up was even slower, for at the latter there were only four adults, and no larvae at all. When immigration is slow, it is not surprising that it takes a long time for numbers to build up. Among the first few adults to arrive there will seldom be a male and female together on one plant, so that unless females have previously been fertilised, they will have to await the arrival of a male before breeding takes place. After the first spraying, it was a month before adults were found and then only three on separate plants. Eggs and small larvae were not observed for another week, and even after six weeks there were insufficient larvae to produce any serious damage. Between the second and third treatments, immigration seems to have been slower still, and no breeding had occurred after six weeks.

Experiment 7. Field trial at Honiara with dieldrin.

In order to put dieldrin to a further test, a block of 55 young palms at 30-ft. spacing in six rows, at the beach-head adjacent to the Government buildings in Honiara, on Guadalcanal, was selected. This plot was about a mile or more from the nearest area with mature coconuts.

The palms were about four years old, but were still small owing to very heavy attack by *Brontispa*, such that in many palms scarcely any green areas remained on the fronds after they were fully opened (Pl. XI, fig. 1); this had resulted in the deaths of one or two of the palms in extreme cases.

On the 18th April 1956 half of the plot (27 palms) was treated with 0·15 per cent. dieldrin, and again thereafter at fortnightly intervals; the remaining 28 palms were left untreated as controls. At the time of each treatment, assessment of the effect of previous treatments was made by classification of the damage to the youngest opened frond. At the start of the experiment, all fronds showed damage, which was severe in 48 out of the 55 palms, and the extent of damage was similar in the treated and control areas (Table XI); the subsequent history can be seen from Table XI and fig. 4.

In the treated area, palms with severely damaged fronds were reduced from 24 to 16 between the first and second treatments, and to 8 by the time of the third treatment; after that no instances of severe damage occurred; by the

eleventh treatment even slightly damaged palms had been reduced to 0, but increased again afterwards, probably because the tenth treatment was given a week behind schedule, which allowed enough immigration from the control area to cause some slight damage.

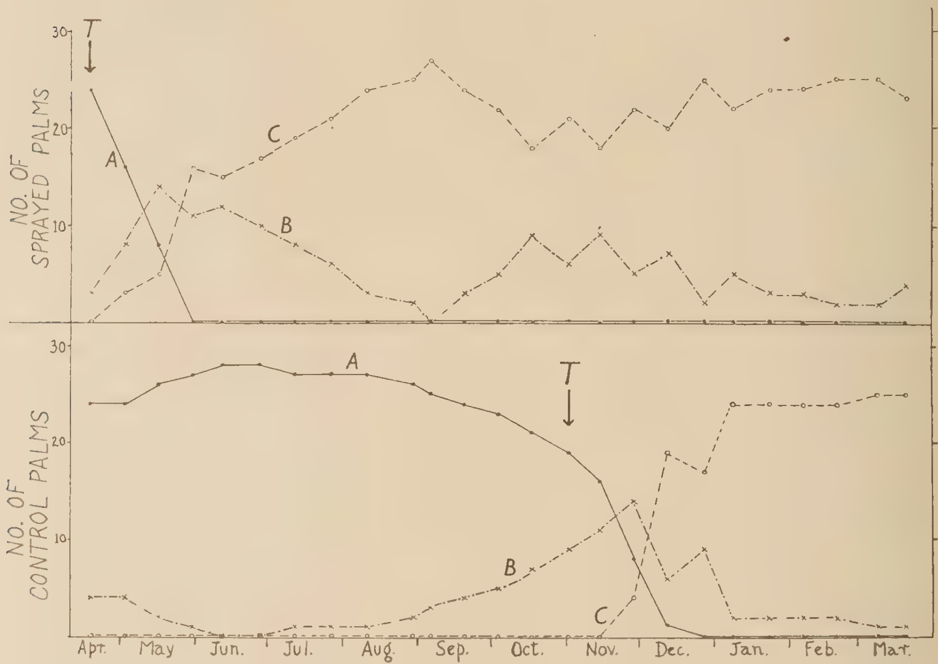

Fig. 4.—Damage counts in field trial with dieldrin at Honiara (Experiment 7). Upper graph: palms sprayed throughout experiment. Lower graph: palms left unsprayed until 1st November. A, palms with severe damage; B, palms with light damage; C, palms without any damage; T, date of first spray treatment.

The palms in the control area were left unsprayed for the first seven months of the experiment. Thereafter they also were sprayed together with the others. During the period for which they acted as controls the condition did not alter appreciably, although from September to October there was a steady decline in the numbers of severely damaged palms (fig. 4). This may have been due to the effect of continued spraying of the other half of the plot, causing a decrease in total numbers of *Brontispa*; or it may be that a prolonged drought provided conditions unfavourable to the beetle.

From the fourteenth fortnight, when spraying of the control area started, it will be seen from fig. 4 that subsequent developments were very closely parallel to those in the sprayed area at the start of the experiment, in that, by the time of the fourth treatment, palms with severely damaged fronds had been almost completely eliminated, and no severe damage occurred afterwards.

From the eighteenth fortnight onwards the interval between treatments was increased from a fortnight to six weeks. It will be seen that this had little if any effect on the excellence of the results; by the close of the experiment at the 24th fortnight, 48 out of the 53 remaining palms (two had died in the control plot during the course of the experiment as the result of *Brontispa* attack) showed no damage to the youngest open frond, and the remaining five only light damage.

With the whole plot treated, so that there was no control area to act as a source of infestation, and under the conditions of isolation from other coconuts of this particular plot, treatment every six weeks therefore seems quite adequate.

The visible beneficial results of treatment in this trial were very striking. When control had been achieved, new fronds as they unfolded showed no damage, and the contrast between the green colour of these fronds and the scorched

TABLE XI.

Field trial (Experiment 7) with 0·15 per cent. dieldrin on a plot of 55 palms at Honiara.

Fortnights after first treatment	Dates of examination of palms : "S" indicates treatment applied also		27 palms treated throughout			28 palms untreated until 1.xi.56		
			Severe damage	Light damage	No damage	Severe damage	Light damage	No damage
0	18.iv.56	S	24	3	0	24	4	0
1	2.v.56	S	16	8	3	24	4	0
2	16.v.56	S	8	14	5	26	2	0
3	30.v.56	S	0	11	16	27	1	0
4	11.vi.56	S	0	12	15	28	0	0
5	27.vi.56	S	0	10	17	28	0	0
6	11.vii.56	S	0	8	19	27	1	0
7	26.vii.56	S	0	6	21	27	1	0
8	10.viii.56	S	0	3	24	27	1	0
9	29.viii.56	S	0	2	25	26	2	0
10	5.ix.56	S	0	0	27	25	3	0
11	19.ix.56	S	0	3	24	24	4	0
12	3.x.56	S	0	5	22	23	5	0
13	17.x.56	S	0	9	18	21	7	0
						Spraying started		
14	1.xi.56	S	0	6	21	19	9	0
15	14.xi.56	S	0	9	18	16	11	0
16	28.xi.56	S	0	5	22	8	14	4
17	12.xii.56	S	0	7	20	1	6	19
18	27.xii.56		0	2	25	0	9	17
19	8.i.57		0	5	22	0	2	24
20	23.i.57	S	0	3	24	0	2	24
21	6.ii.57		0	3	24	0	2	24
22	20.ii.57		0	2	25	0	2	24
23	9.iii.57	S	0	2	25	0	1	25
24	20.iii.57		0	4	23	0	1	25

The figures indicate the numbers of palms showing the specified extent of damage to the youngest open frond on the dates indicated. Reductions in numbers in the control plot on 14th and 28th November 1956 were due to the deaths of two palms.

appearance of those which had unfolded before treatment was started, was very impressive (Pl. XI, figs. 2 & 3). The longer the treatment went on, the more undamaged, green fronds appeared, with clearly beneficial effects on the general health of the palms. The contrast between damaged and undamaged foliage could sometimes be seen on one and the same frond; each frond starts to unfold and to become vulnerable to attack by *Brontispa* in the apical part first, so that in cases where the first treatment was administered when the apical part of a frond only had been attacked the basal part was protected and escaped damage (Pl. XI, fig. 4).

TABLE XII.

Experiment 8—Counts of *Brontispa* in trial of imitation "aerial spray" with 0·15 per cent. dieldrin, applied at fortnightly and monthly intervals.

Dates of counting				15.v.56				29.v.56			26.vi.56			24.vii.56			21.viii.56			18.ix.56			17.x.56			15.xi.56			10.xii.56		
		No. of plots	No. of palms	Adults	Larvae	Adults & larvae	First treatment, 16th May (all plots)	Adults	Larvae	Adults & larvae	Adults	Larvae	Adults & larvae	Adults	Larvae	Adults & larvae	Adults	Larvae	Adults & larvae	Adults	Larvae	Adults & larvae	Adults	Larvae	Adults & larvae	Adults	Larvae	Adults & larvae	Adults	Larvae	Adults & larvae
Treated plots	Fortnightly	3	88	1	0	1		2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Monthly	1	36	8	0	8		11	8	19	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
	Fortnightly and Monthly	4	124	9	0	9		5	2	7	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Control plots		3	88	2	14	16		2	16	18	7	14	21	3	25	28	9	3	12	2	0	2	0	0	0	0	0	0	11	2	13

Only living insects are recorded, and the figures represent the number of insects per 100 palms, to the nearest whole number.

Experiment 8. Imitation "aerial spray" trial with dieldrin.

In the experiments described so far the method of application has involved individual treatment of the palms.

Although aerial spraying is unlikely ever to prove necessary for the control of *Brontispa* on mature palms, this method of applying insecticide might conceivably be employed against other pests (*e.g.*, *Amblypelta cocophaga* China), and it seemed worth while to carry out a further small trial at Kukum to try to obtain some indication of how effective aerial spraying might be in controlling *Brontispa*.

Application was by means of the same stirrup pump and lance equipment as was employed in the other Kukum experiments but it was used in a different way. Instead of directing the spray straight at the central spike, the lance was held high in the air so that the spray spread out and fell as a rain on to the palms; the effect was to simulate approximately a spray application from an aircraft.

Four plots were treated, and three left untreated as controls. Of the treated plots, three (two of 36 palms each and one of 16 palms) were given fortnightly treatment and one (of 36 palms) was given monthly treatment. Of the three control plots, two were of 36 palms each and one of 16 palms. Assessment of results was made only by counts of *Brontispa*. Counts were made the day before, and a fortnight after the first treatment, and thereafter at monthly intervals, in every case just before a treatment.

The figures are shown in Table XII. Although not so impressive as in Experiment 5, they do show that treatment was to some extent effective, in that from the second month after treatment, onwards, *Brontispa* was kept down to negligible numbers, and larvae were eliminated altogether. In the control plots some numbers were found, including larvae, up to the fourth month after treatment; they then almost completely disappeared for three months, but this was almost certainly due to conditions of severe drought which had prevailed ever since the palms were planted, and from which they did not completely recover, few fresh fronds being produced and some of the palms even dying; in December, after rain, many of the palms recovered and insects appeared again.

More convincing are the total numbers of dead *Brontispa* compared with living ones in the treated plots on the one hand, and in the control plots on the other, after treatments had started. Calculated as the number per 100 palms, the figures were as follows:—

	Treated palms	Controls
Living	9	94
Dead	13	1

This, coupled with the evidence of suppression of larvae and therefore of breeding, leads us to conclude that aerial spraying would exercise a large measure of control of the *Brontispa* population in addition to its effect against other pests.

Control of *Brontispa* under Field Conditions.

The work so far described was all carried out under carefully controlled conditions on relatively small plots of seedling palms.

Since 1954, various more extensive areas of new planting or underplanting of areas of old palms have provided opportunities for confirming, on a larger scale, the results of the plot trials.

The following paragraphs summarise the results of these further tests, all carried out in the Russell Islands.

(1) *Island of Talina.*—An area of about 100 acres of mature palms was destroyed during the war. In 1954 this area was replanted. Although the seed nuts were of local origin and therefore relatively resistant to attack, extensive

patches of *Brontispa* damage soon appeared; one estimate indicated that something like 2,000 young palms were severely affected.

Spraying every fortnight with 1 per cent. Pespruf (0·2% DDT), using Rega atomisers, quickly brought the attack under control. After about three months there was no longer any need for regular spraying, and the beetle has been prevented from causing any further severe damage by the timely application of Pespruf whenever isolated patches of damaged palms appear in the area. Beetle damage is now (November 1957) kept down to negligible proportions throughout the whole block of 100 acres.

(2) *Island of Hui.*—A further 50–60 acres of young palms have been planted on this small island. Here, spraying was commenced as soon as *Brontispa* began to appear and there has never been sufficient severe damage to cause any concern. Regular spraying of the whole area has never been necessary and treatment is confined to those patches where obvious damage has occurred. The palms are at present inspected about every two months and this frequency has proved sufficient to prevent *Brontispa* from becoming established in any strength. Either Pespruf or Rulene (a similar but more concentrated DDT formulation) has been used throughout.

The use of DDT in preference to dieldrin was initially fortuitous. Supplies of Pespruf were on hand when spraying commenced, and since very satisfactory results were being obtained there seemed little point in switching over subsequently to the slightly more effective but also more expensive dieldrin treatment.

(3) *Banika Estate—Fiji × Malayan dwarf palms.*—A consignment of seed nuts from Suva were planted in March 1956 beneath an existing stand of mature and beetle-infested palms. It was soon apparent that this new dwarf variety was as susceptible as the Malayan tall palms and regular spraying was necessary from the time the young palms were about three months old. Owing to the constant reinfestation from the old palms, spraying has had to be carried out about once every month; at this frequency, severe damage is almost entirely avoided. In this case, preference has been given to dieldrin, which is applied with the Rega atomisers, and every young palm is regularly treated.

(4) *Banika Estate—Malayan palms, replanting experiment.*—At the beginning of 1957, 1,280 Malayan seedlings were planted out beneath 18 acres of 50-year-old palms. Planting was completed by the middle of April and a month later a start was made with the destruction of the old palms by poisoning. By the end of June, the crowns of the old palms had died and the *Brontispa* population diverted its attention to the seedling palms below. A really devastating attack developed and, despite prompt application of dieldrin, a number of seedlings had at least one young frond completely destroyed by invading adults. Both dieldrin (15%) and Eldrinol (containing 25% dieldrin) have been used on this experiment. The insecticide has largely prevented breeding on the young palms and, although up to 20 dead adults have been collected from between the leaflets of a single frond, very few larvae have been found. Spraying is being continued. In order to speed up the work, the 1-pint (568 cc.) size Rega atomisers have been replaced by knapsack sprayers of $2\frac{1}{2}$ gallons' capacity fitted with low-volume nozzles which enable one labourer to deal with about 600 young palms in four hours using about three gallons of spray.

Summary.

An account is given of the damage caused by adults and larvae of *Brontispa longissima* (Gestro) to the young unopened fronds of coconut palms in the British Solomon Islands. Normally, only young palms less than 10 years old are severely attacked, but this has interfered seriously with replanting programmes. Full-grown palms suffer severe damage only occasionally; reasons for this difference in susceptibility are suggested.

Earlier reports, that seedlings of Malayan type are more readily and severely attacked than those of Samoan or local origin, were confirmed. A fertiliser treatment had no effect on the growth of the palms or the amount of damage by *Brontispa*.

Laboratory tests showed that the deposit from a spray of 0·2 per cent. p,p′DDT was completely effective for three–four weeks, that chlordane (0·16%) became significantly less effective in the third and fourth weeks, and that dusts of DDT, alone and with BHC, showed signs of diminished efficiency in the fourth week.

In small-plot trials with sprays of DDT or chlordane, applied at various concentrations and frequencies, the effects of treatment were assessed by counts, at suitable intervals, of living and dead examples of *Brontispa*, by estimating damage to the youngest open frond, and by measuring the growth of seedlings. DDT at 0·1, 0·2 and 0·3 per cent. of p,p′isomer, and chlordane at 0·08, 0·16 and 0·24 per cent. gave very satisfactory control of a heavy attack of the beetle and suppression of damage. Applications at 10-day intervals were more effective than 3-weekly ones. Similar trials with dieldrin at 0·1 per cent. and DDT at 0·3 per cent. against a light attack were completely effective.

In further trials, direct comparisons were made between DDT at 0·25 and 0·025 per cent., chlordane at 0·16 per cent. and dieldrin at 0·15 per cent. applied at both fortnightly and monthly intervals. The lower concentration of DDT was much less effective than the other treatments. DDT at the higher concentration and dieldrin were equally effective when applied at fortnightly intervals, but at monthly intervals the latter was superior in control of immigrant beetles. This is attributed to its greater persistence. It is concluded that, in the formulations used in this trial, dieldrin is superior to DDT and chlordane.

Further trials with dieldrin at 0·15 per cent. showed that palms subjected to only moderate reinfestation were adequately protected by spraying every six weeks, whilst isolated areas of young palms may be left much longer, probably several months, once the initial population has been controlled. The maximum frequency, under the most adverse conditions, might vary between 2 and 4 weeks, initially. Varietal susceptibility in the coconut does not affect the efficiency of control.

Slight phytotoxicity, indicated by retardation of growth and rate of production of new fronds, was caused by frequent applications of high volumes of spray, but the volume necessary to produce such effect is considerably in excess of that required for satisfactory control. Unnecessarily high volumes and concentrations should, however, be avoided.

The spray was applied to each palm, individually, downwards on to the central spike, where the beetle lives. Equipment capable of delivering a fine, low-volume spray controlled by an efficient trigger tap will use only about 16 cc. spray per palm up to 3 years old. With a low-volume atomiser, this consumption can be reduced to about 6 cc.

An imitation aerial spray gave promising but inconclusive results.

With the proprietary formulations of insecticides used, the addition of a wetting agent was unnecessary.

Field applications were tried out in the Russell Islands on extensive areas of young palms that showed heavy beetle attack. Sprays containing dieldrin or DDT, each in two proprietary formulations, gave excellent and satisfactory results, respectively.

It is concluded that the experiments clearly indicate that very satisfactory control can be achieved at low cost, and that a programme of replanting could be safely embarked upon without fear of the severe losses, due to *Brontispa*, that have been suffered in the past.

Acknowledgements.

We are indebted to Messrs. Unilever, Limited, for permission to publish the results of the various experiments carried out in the Russell Islands.

We would like to express our thanks to the Senior Agricultural Officer, British Solomon Islands Protectorate, for help in a number of ways and especially for providing facilities and the necessary labour to maintain the experimental plots at Kukum; and to Mr. P. G. Fenemore for kindly continuing routine recording of data during the last two or three months for certain of the experiments on Guadalcanal.

We also wish to thank Dr. H. G. H. Kearns for much helpful advice and the provision of equipment and of the DDT formulation used in Experiment 4 at Kukum, and to record our appreciation of the advice regarding the conduct of the earlier work which was afforded us by the late Dr. J. S. Phillips.

We acknowledge our gratitude to the Shell Petroleum Co., Ltd., for their generosity in defraying the cost of the coloured plate (Pl. XI).

We are indebted to the following Companies who provided samples of their products for use in the experiments:—Messrs. Imperial Chemical Industries (Australia & New Zealand), Ltd., The Shell Company of Australia, Ltd., and Houghton & Byrne Proprietary, Ltd. (Sydney).

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FIG. 1. Adults on coconut leaflet, showing linear feeding scars on the latter (× 3).

FIG. 2. Three eggs on coconut leaflet surrounded by feeding débris of adults (× 22).

FIG. 3. Full-grown larva (× 8).

FIG. 4. Pupa, from above (left) and below (right) (× 8)

STAGES IN THE LIFE HISTORY OF *BRONTISPA LONGISSIMA*.

FIG. 1. Fresh feeding scars on surface of leaflet; their linear form and parallel arrangement should be noted.

FIG. 2. Part of a damaged leaflet after opening of frond, showing spread of necrotic area and deterioration of frond.

FIG. 3. Older fronds from mature palms; severely damaged (left) and undamaged (right).

FIG. 4. Mature palm severely damaged by *Brontispa*, with undamaged palm next to it.

DAMAGE CAUSED TO COCONUT FRONDS BY *BRONTISPA LONGISSIMA*.

FIG. 1. Varietal resistance trial; coconuts planted out in plots, Ufa Estate, Russell Islands.

FIG. 2. Seedling of local Solomon Islands type, six months old, showing fronds divided into leaflets.

FIG. 3. Seedling of imported Malayan type, six months old, showing entire, undivided fronds.

FIG. 1. Plot of young coconut palms sprayed with 100 cc. per palm of 0·24% chlordane (as "Octa-Klor") every ten days, showing undamaged fronds; Ufa Estate, Russell Islands.

FIG. 2. Control (unsprayed) plot on Ufa Estate, showing raggedness of fronds caused by *Brontispa* attack, and poor growth of palms (*cf*. fig. 1).

FIG. 3. Method of spraying young coconut palms in experiments at Kukum, Guadalcanal, with stirrup pump and lance.

FIG. 4. Method of measuring height of palms.

FIG. 1. An untreated young coconut palm heavily attacked by *Brontispa longissima*; Honiara.

FIG. 2. Palm from same plot as that in fig. 1, five weeks after the first spray treatment with 0·15% dieldrin.

FIG. 3. The same palm as fig. 2, three months after the first spray treatment with 0·15% dieldrin.

FIG. 4. A single frond of a palm five weeks after the first spraying with 0·15% dieldrin, showing damaged apical and protected basal areas.

CONTROL OF *BRONTISPA* BY DIELDRIN.

ENUMERATING POPULATIONS OF ADULTS OF THE RED LOCUST, *NOMADACRIS SEPTEMFASCIATA* (SERVILLE), IN ITS OUTBREAK AREAS IN EAST AND CENTRAL AFRICA.

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The International Red Locust Control Service exists to control this species, *Nomadacris septemfasciata* (Serv.), in its outbreak areas; there is reason to believe that if that objective is achieved, plagues of the species will be prevented (Uvarov, 1951; Gunn, 1952, 1957). The outbreak areas in question are grouped in three regions: the flood plains of Lake Mweru wa Ntipa in Northern Rhodesia, the flood plains of Lake Rukwa and certain other connected flood plains to the north-west in the Rukwa Rift Valley of Tanganyika Territory, and the flood plains of certain tributaries of the Malagarasi river in Tanganyika. They total about 2,000 sq. miles of grassland and accounts of them have been given by Michelmore (1939), Burnett (1951), Pielou (1952), Vesey-FitzGerald (1955), and Backlund (1955, 1956).

Each area is, in general, surrounded and marked off by forest, swamp, and open water; there is evidence from Michelmore's unpublished reports to the Committee on Locust Control of the Economic Advisory Council (1933–37) onwards that diffuse populations of the locusts remain in these circumscribed grasslands and do not, in general, enter the forest and emigrate, but that concentrated swarms of the locusts characteristically migrate, roost in the trees, and if left alone, eventually emigrate. Up to the point at which emigration of swarms occurs, therefore, several of the areas support separate populations which do not seem to lose much to the outside or to gain from it. There seems, therefore, to be an opportunity of repeatedly estimating the sizes of the populations of at least some of the areas, primarily to discover what control measures are required and to assess the effects of the measures taken. With sufficiently refined methods, the extent of multiplication at breeding, the effects of physical and biological factors of the environment, and so forth, could also be investigated.

The smallest of the important outbreak areas that is suitable covers 110 sq. miles and the largest about 600 sq. miles, and they are by no means homogeneous. That is to say, the physical labour required for population assessment is substantial but it cannot be avoided by, for example, the use of a few small sample plots, because considerable variations and changes of density and movements of the locusts occur within an outbreak area, even with diffuse populations. The present paper describes attempts to enumerate the locust populations in complete outbreak areas and gives some of the results and conclusions. There is no pretence that the methods are satisfactory, but a start has been made.

Estimates of total locust populations over large areas have not previously been attempted. The obvious method of doing it is to take adequate samples to find the density per unit area and then multiply by the total area. Estimates of density of diffuse populations have been made, for example, on the Brown Locust, *Locustana pardalina* (Wlk.), over areas of a few acres (Smit, 1939) and on the Desert Locust, *Schistocerca gregaria* (Forsk.), over large areas (Ramchandra Rao, 1942), but without interpretation into total populations. These estimates

depended on being able to see each locust, at any rate if it made a slight movement. The tall grass of the Red Locust habitat usually hides most of the insects, unless they fly up. For the same reason, photographic methods are out of the question (Gunn, Perry & others, 1948; Callaway *in* Gunn, Lea & others, 1948).

Methods.

The basic datum is the number of locusts that fly up at the approach of the observer. The very few locusts that can be seen clinging to the grass are also included. Under suitable conditions, a majority of the locusts in the general line of advance of the observer do take to the wing but it is quite clear that not all of them do, for another observer coming 100 yd. behind and exactly along the same line always flushes some more. The counts obviously give only a reliable *minimum* estimate. No direct method has been found of counting the locusts that do not fly up; mostly they are not seen because they drop between the stems of the dense tall grass and run along on the ground between the bases of the tufts. They have to be allowed for by some indirect method.

Line sampling was adopted intuitively in preference to random sampling at points. Mr. J. G. Skellam of the Nature Conservancy has rationalised this by pointing out that if sample points were determined by random numbers, the travelling time between points would be wasted and, moreover, it would be very difficult to locate the points accurately in the open plains. The locusts have a gregarious distribution, in the statistical sense, and choice could easily creep in if points could not readily be located accurately.

The sampling lines should be chosen without regard to the nature of the vegetation or terrain, up to the limits of the grasslands, so as to cover the area with a well-distributed pattern. Because of impassable rivers, however, the whole area has to be divided into sectors within which movement is possible in

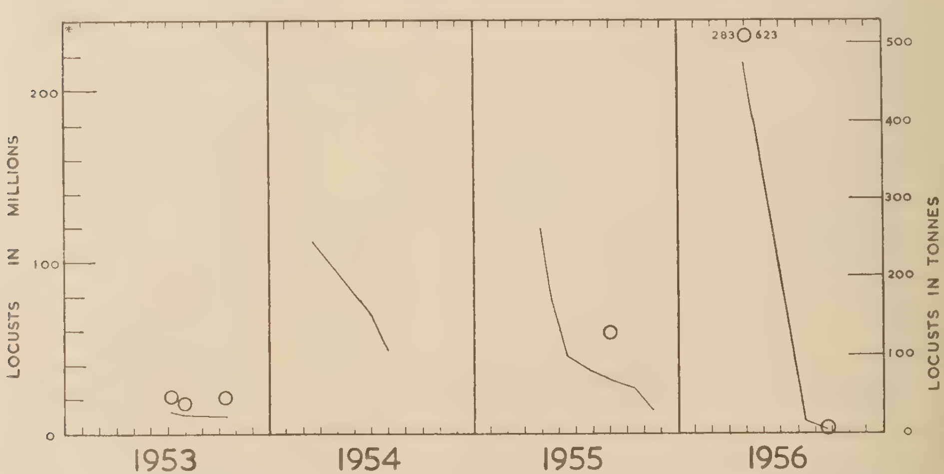

Fig. 1.—Numbers of adults of the Red Locust estimated by counting from a vehicle in three (189 sq. miles) of five sectors (253 sq. miles) of the North Rukwa Outbreak Area (lines) and in the five sectors (circles). In each year, the population was reduced by insecticide spraying and the increasing steepness of the reduction in successive years is due to a change in method of application, from heavy ground machines to light aircraft. The steep little drop at the end of 1955 is probably due to reduced activity in females about to lay eggs and not a real fall in population. The approximate weights given on the right are based on provisional average locust weights supplied by Dr. R. F. Chapman: male—1·9 g., female—2·5 g., and a sex ratio of unity. We are indebted to Mr. A. J. M. Carnegie for the 1955 data.

all directions. The programme is therefore laid out on a map which shows the forest and lake edges and the rivers, the object being to plan a uniform intensity of sampling all over the area. An intensity of one running mile per three sq. miles seems to be adequate (fig. 1) and this means that the actual number (minimum) of locusts is counted on nearly 0·04 per cent. of the area (see next paragraph). Each sector is divided into rectangles, such that the diagonal of each in miles is one third of the area in square miles, and the diagonal is taken as the sampling line. For example, if the rectangle is more than 5 miles long, its width must lie between 3 and 3¼ miles to achieve this and a reference table has been made up to indicate the proper shape at each size. Having marked on the map the chosen sampling lines, it requires some skill and assiduity to navigate along them. The sampling lay-out is altered at each assessment so as to avoid formation of beaten tracks and altering the distribution of the locusts.

Only those locusts are counted that fly up in a limited width of strip. Most of the assessments have been done from a Land Rover, of overall width nearly 2 yd. The man counting has to judge whether or not each locust flying up started from within that width in front of the vehicle. He can be helped by strips of paper stuck on the windscreen but these increase errors if he moves his head. The speedometer is a special one, showing continuously moving hundredths of a mile, so that unit samples of 0·1 mile can be accurately measured. In suitable terrain, it is possible to complete a 250 sq.-mile area in a week, providing 850 × 0·1-mile samples, and to work them up in a day or two. The Land Rover cannot be used on very rough ground or when there is much surface-water and, until 1956, scouting on foot had to be resorted to under these circumstances.

In that year, however, trials were made (C.C.S.) of scouting with an amphibious vehicle, the Swamp Skipper. This has as its wheels water-tight steel drums of 7-ft. diameter and 3-ft. width, so that the vehicle normally rolls but will also float, with slow progress. The observer's seat is placed on the roof, so that eye level is 15 ft. above ground and thus above even the tallest grass. In this case, counts are made of the locusts that flush from within the width of the vehicle up to the insides of the wheels, a distance of 2 yd.

If linear counts of locusts that are flushed by the observer are to be of substantial value, two observers of a single area must arrive at similar estimates independently, even though background conditions for the two estimates are not the same. The aim should therefore be to find the absolute total number of locusts and not merely some proportional figure. Attention must evidently be directed to the conditions that affect the proportion of the locusts that are flushed.

Errors and Variations.

Estimates of error have not been satisfactory. Mr. Skellam visited the Rukwa Valley in 1954 to advise on the matter and concluded that, in spite of the patchiness of the distribution of the locusts, a root mean square deviation could be used for finding the standard error of the mean, but that it was the systematic errors rather than the random errors that gave cause for concern. His account of the matter is expected shortly.

Temperature.

It is quite common for the Red Locust in the outbreak areas to experience air temperatures so low as absolutely to prevent flight. We are indebted to Dr. R. F. Chapman of this Service for as yet unpublished data about behaviour in relation to temperature. At body temperatures below about 20 or 21°C. the locusts cannot fly; if disturbed under such conditions, they commonly flap their wings (fanning) without taking off, or they drop to the ground between the grass stems. At an air temperature of 22°C., they can fly and do occasionally do so

spontaneously. Spontaneous flight is maximal at air temperatures between 29 and 35°C., while at higher temperatures it falls off rapidly. Counts of locusts that are stimulated into flight should therefore never be made below 22°C., or above 35°C. In practice, when there is much spontaneous flight, counting becomes difficult and the most convenient range is about 23 to 30°C.

It has been found by several authors, most recently by Davey & Johnston (1956) for *Locusta*, that when a particular area of presumed fairly homogeneous infestation is traversed repeatedly by a man on foot, the number of locusts flushed per unit time or distance at first rises as the air temperature rises and then remains reasonably steady, in spite of further rises in temperature. They take the view, however, that the influence of temperature varies with the type of habitat and they produce some evidence for this. Dr. Chapman has found, in scouting on foot, that there is a deficiency in numbers flying up at low temperatures and that there does seem generally—though not always—to be an increase until the air temperature approaches 35°C.; but, in other observations, he has also found an adaptation to temperature so that when high temperatures are reached slowly they do not have so much of an activating effect. We have as yet few data on the effect of temperature on the percentage of locusts that flush right in front of an advancing vehicle; this may be quite different from the effect on locusts up to many yards to the side of the observer, which have always been included by previous workers when scouting on foot.

Wind.

A very striking inhibitory effect is produced by even moderate winds; in repeated assessments of the locusts in a particular square mile in June 1955, the results in Table I were obtained. Wind speeds were taken after every half-mile

TABLE I.

Effect of wind speed on numbers of locusts flushed in ½-mile counts in repeated tests in a particular sq. mile on two successive days.

Wind	Locusts flushed		Temperature range (°C.)	Number of half-mile counts
	Range	Average		
> 5 m.p.h. ..	57—252	172	24·4—31·7	25
about 5 m.p.h.	146—966	332	26·7—31·7	6
< 5 m.p.h. ..	600—1440	1019	22·8—29·4	14

The wind was entirely below or entirely above 5 m.p.h. in most of the observations, but in those classified as "about 5 m.p.h." it oscillated around 5 m.p.h., mostly at higher speeds.

on an anemometer giving direct readings of speed and on each occasion the highest and lowest speeds over a 100-second reading were noted. Detailed examination of these and other results indicated that assessments ought not to be made when wind speeds go over 5 m.p.h. and that lesser winds had little effect. In the same data, there was an inverse but insignificant correlation between locusts flushed and temperature.

Vegetation.

It is to be expected that the proportion of locusts flushed would vary with the nature of the vegetation. The ground may be completely bare, either in patches of a few square yards or over square miles, or the grass may form a dense cover up to nearly 8 ft. high—commonly it is 3–6 ft. No simple and effective method of

assessing influence of grass height has been found; such indications as have been obtained suggest surprisingly little influence, but they are somewhat ambiguous.

Condition of the locusts.

Locusts that are teneral, or copulating, or females that are nearly ready for oviposition are very difficult to flush, and no useful estimates of a population can be made if it contains many individuals in any of these conditions. An example of the effect of readiness to lay eggs on the apparent size of the population is seen in fig. 1 in the estimate for November 1955.

Density of locusts.

Difficulty in counting begins to arise when there are more than 100 locusts per 0·1 mile. When the number enters the thousands it is virtually guessed, but considerable repeatability can be attained by experienced men. The best test of this is to assess a complete population before and after the pre-oviposition dispersal (see p. 280).

Calibration.

Many attempts have been made by various members of I.R.L.C.S., especially Mr. D. Vesey-FitzGerald, Mr. I. A. D. Robertson and Mr. J. Haydn Lloyd, as well as visitors (Prof. O. W. Richards (1953), Mr. J. G. Skellam), to get precise information about the hidden population, by repeated flushing, by marking and recapture, and by drench spraying and corpse counting. None of them has given sufficiently satisfactory results. They have, however, gradually led to the interim conclusion that, in reasonable flushing weather, about 60 per cent. of the locusts normally fly up in the path of a Land Rover.

Burnett's (1951) conception of the " equivalent strip " is convenient here; the phrase refers to the width of the strip of grassland in which the total population, seen and unseen, is equal in number to the locusts actually counted. In counting flushed locusts in front of a Land Rover about 2 yd. wide, the equivalent strip (e) is then about 1·2 yd.

It is evident that if the value of the equivalent strip has not been determined accurately even under favourable conditions, it is not possible to rely on the precision of estimates of total numbers of locusts, particularly since the value may vary according to temperature, wind speed, height of grass, condition of the locusts, and so on. It does seem, however, that if the counts are made only in " good flushing weather " and when the locusts are not sluggish because of being teneral or about to lay eggs, the results may be reasonably repeatable. For example, in our original and inexperienced tests in 1953 we separately estimated the total number in the North Rukwa Area (253 sq. miles), getting 21 million on 3rd–12th July and 18 million on 12th–25th July. A third trial (19th–27th October), after 2–3 million locusts had been claimed as destroyed, gave 21 million (e = 1·2 yd.). Again, in September 1956, one experienced man and one inexperienced man simultaneously fully sampled the same outbreak area on parallel lines two miles apart; with an estimated total of only 2½ million locusts, the average counts were 0·59 and 0·57 locusts per 0·1 mile and the difference between these two averages was less than its standard error. When the standard error has been worked out it has usually been about 10 per cent. of the mean. That is to say, in spite of all the uncertainties of population assessment from a vehicle, the method does distinguish clearly between very different populations. It can be seen from fig. 1 that reasonable consistency has been obtained.

Distributions.

The nature of the distribution of the locusts in a complete outbreak area has received some attention. When the population is small, the counts might follow

a Poisson distribution. In September 1956, with 1,278 counts of 0·1 mile over the whole of the North Rukwa Area, averaging under 0·6 locust per count, there were none in 71 per cent. of the counts, compared with a Poisson expectation of about 55 per cent., there were fewer ones and twos than in the Poisson distribution and more of the higher numbers, and chi squared was right off the table. With a maximum of 11 locusts in a 0·1-mile count, there could hardly be much question of the locusts reacting gregariously to one another. The distribution was, however, gregarious or clumpy in the statistical sense, presumably reflecting the influence of patchiness of vegetation on either survival or, more probably, behaviour.

When one examines data from larger populations in the same area, there is never any question of the counts being normally distributed. There are always too many zeros and also too many counts far above the average. Even if one plots frequency against the logarithms of the counts, the graph rarely resembles a normal curve in any way, being much too flat.

There is little doubt that parts of the outbreak area are virtually completely evacuated as the dry season progresses and that in other parts locusts at first tend to remain when they enter them; once such a retentive place becomes sufficiently densely populated for the locusts to react to one another, then a swarmlet tends to form and the retentiveness of the place may be either increased or eventually overcome by the gregarious and migrant behaviour of the locusts. The distribution of the locusts tends then to be strongly gregarious in both behavioural and statistical senses.

Changes of Population Density: Concentration.

Locusts are dangerous to crops outside the outbreak areas only when they form gregarious swarms and emigrate. It has sometimes been thought that the formation of swarms of adults depends on concentrated egg-laying leading to the formation of dense hopper bands. Swarms can arise in this way but in the Red Locust they can also form from scattered adults progressively congregating throughout the dry season. The distribution of counts of locusts flushed per tenth of a mile by the Land Rover at three periods in 1953 is shown in Table II.

TABLE II.

Distribution of densities of Red Locusts in North Rukwa Outbreak Area in 1953, estimated as numbers flushed in a two-yard strip in one-tenth of a mile line-samples, in front of a Land Rover.

	Early July		Late July		October	
Counts per 0·1 mile	% frequencies	% locusts	% frequencies	% locusts	% frequencies	% locusts
0	47·27	0	47·59	0	59·28	0
1—40	50·70	75·9	50·94	80·9	37·25	42·3
41—80	2·02	23·4	1·15	12·5	1·13	11·5
81—120	0·05	0·7	0·30	6·6	1·59	27·9
121—160	0	0	0	0	0·56	13·8
161—200	0	0	0	0	0·12	4·4
	100·04	100·0	99·98	100·0	99·93	99·9

Over 1,000 samples at each assessment, distributed over about 250 sq. miles. Total population about 20 million throughout the year. Weighted for uneven sampling.

Between the two assessments in July, the results suggest an increase in locusts at 81–120 per count at the expense of those at 41–80; the locusts were, in fact, moving about a good deal at the time, but by and large the two assessments confirm each other by their similarity and the differences are insignificant. By October, however, the area that showed no locusts at all had increased, and counts over 120, which had not been recorded at all in July, accounted for over 18 per cent. of the locusts. In October, nearly half of the locusts were at the higher densities (over 80) that accounted for less than 10 per cent. of them in July. The changes are highly significant and nothing is known or suspected to suggest that they are not real and representative.

The full picture is not revealed by these figures, for before the October assessment, over 10 per cent. of the densest locusts had been destroyed by insecticides on 0·6 per cent. of the area and the number of corpses estimated by Mr. J. H. Lloyd. This control could not increase the number of zero counts to a greater extent than it reduced the highest counts, even if the spraying methods in use produced 100 per cent. clearance; without the spraying, there would have been still more of the highest counts and fewer of the low counts. There had thus undoubtedly been a concentration of the locusts, although the population was very low, averaging only about 100 locusts per acre over the whole area. In October, the highest count of 200 in 0·1 mile represented a mean density over that particular sample of only one locust per sq. yd., though parts of the sample would contain denser locusts.

In 1954, there were at first at least ten times as many adult locusts as in 1953 but it was not possible to assess the whole North Rukwa with a Land Rover, because of persistent flooding in about 25 per cent. of the north-eastern part of the Area. The remainder (189 sq. miles) was assessed in March and in August (Table III). With much higher densities than in 1953 (mean 1,000 locusts per

TABLE III.

Distribution of densities and numbers of Red Locusts in part of North Rukwa in 1954.

	March			August		
Counts per 0·1 mile	% frequencies	% locusts	Locusts (millions)	% frequencies	% locusts	Locusts (millions)
0	4·1	0	0	39·0	0	0
1—32	67·3	20	24	45·8	26	12
33—100	22·4	28	34	12·7	44	20
10^2—10^3	5·9	29	36	2·5	30	14
10^3—10^4	0·3	23	28	0	0	0
	100·0	100	122	100·0	100	46

Weighted for uneven sampling. Compare Table II.

acre in March, reduced to 40 per cent. of this by insecticides by August) the same general picture is seen. The much larger population (estimated at 122 million), with locusts in all but 4 per cent. of the counts in March, had again, a few months later, evacuated over a third of the Area; but it was still more extensive (estimated at 46 million) as well as denser than it had been in 1953.

The average density of all the locusts killed was about 3 per sq. yd., corresponding to a count of 650 per 0·1 mile; between March and August, estimated densities ten times as great occurred and were attacked, and the lowest

densities attacked were at counts of just over 100 per tenth of a mile. Considering the numbers of locusts in millions at each density, those below 100 per count fell between March and August by 26 million and this fall could not have been due to spraying at low densities, because these were not attacked; the locusts had concentrated before being sprayed.

The 1954 population was quite large enough to form migrant swarms. Apart from many swarms that were destroyed just before leaving the outbreak area, one escaped for a time and travelled 75 miles before it was eventually destroyed; it was a small one, possibly containing 5 to 10 million locusts, and weighing only about ten tons. In 1953, on the other hand, after July the locusts did not ever seem likely to emigrate. We thus have now some idea of the numbers at which a population becomes dangerous. There are other data as well which strongly indicate that if adequate numbers of locusts are present, they will eventually concentrate into migrant swarms if left alone.

If one ignores the importance of the locusts as parents of the next year's population within the outbreak areas, the problem is how, at minimum cost, to reduce the numbers to a level at which emigration will not occur in the current year. Now cost depends mainly on the extent of the area sprayed, not at all on the density of the locusts and, when the apparatus is owned by the Service and the men are employed all the year round, not at all on time spent doing nothing. The fact that the locusts concentrate progressively indicates that the correct strategy is to wait until dangerous densities appear and to attack only those. This can be a nerve-racking procedure, because changes in the weather or grass fires can speed up concentration in several areas simultaneously. Since 1955, however, it has been found that the striking power of very light spraying aircraft is sufficient to enable us to allow concentration to go far before attacking (J. H. Lloyd, in press); the changes in distribution of the locusts must, however, be followed closely by quantitative assessments.

Changes of Population Density: Dispersal.

It has been believed for a long time (Lea & Webb, 1939) that Red Locusts disperse before laying their eggs, but until 1956 there were no quantitative data. Since this species is exceptional in that egg-laying occurs mainly at night, it is not easy to see whether they lay in groups or as isolated individuals. In 1956, two Land Rover assessments of population were made in the Iku Outbreak Area

TABLE IV.

Distribution of densities of locusts in Iku Outbreak Area on 28th September and 6th–11th November 1956.

	September			November		
Counts per 0·1 mile	% frequencies	% locusts	Locusts (millions)	% frequencies	% locusts	Locusts (millions)
0	38·8	0	0	24·3	0	0
1 — 9	44·7	14·0	1·7	50·0	18·0	2·1
10 —99	15·0	41·0	4·9	25·0	72·5	8·6
10^2—10^3	1·5	45·0	5·4	0·7	9·5	1·1
	100·0	100·0	12·0	100·0	100·0	11·8

In September, all the high counts were made in a single area of at least 5 sq. miles out of 82 sq. miles; this patch was more heavily sampled but the figures given below are suitably weighted.

in the Rukwa Valley, one in September (C.C.S.) and another in early November by Messrs. J. Haydn Lloyd and W. N. Yule, who have kindly allowed us to quote some of their results (Table IV).

Two sections (Mivunda and Malililo) were not sampled on both occasions by Land Rover, but scouting on foot showed that they were not much involved in the locust movement and, insofar as they were involved, they did not alter the trend of the results. The extent of the patch that contained the bulk of the locusts in September was not determined exactly, so there is some uncertainty about the total number of locusts at that date; the extent given, 5 sq. miles, is a minimum and the results would be even more striking if it was in fact larger. In September, within the concentration area there were continuously counts of over 20 locusts, only 5 out of 55 being below this; 6 counts were over 200 and the average was 43 locusts per 0·1 mile. Outside the concentration area, out of 257 counts there were only 8 of over 20 locusts (the highest being 43) and these higher counts were scattered about; the average was less than 4 locusts per 0·1 mile. The degree of concentration in September was therefore quite striking. In November, there was no discernible single concentration area, there were no counts over 200, and 103 out of 704 of over 20, but these were scattered about all over the place except that there were none of them in the previous concentration area. As Table IV shows, in November the acreage containing no locusts was reduced in extent, and the acreage containing 1–99 was increased, both at the expense of the areas containing over 100 per 0·1 mile.

The November assessment was done soon after the very first shower of rain (3rd Nov.) and before egg-laying began in mid-November. The dispersal would probably have shown even more clearly if the assessment could have been done a little later, but flushing would probably have been reduced because the females were about to lay eggs.

The results do not mean that egg-laying is scattered uniformly over the area; there are undoubtedly conditions that are selected by the locusts (Vesey-FitzGerald, 1955; Backlund, 1955). But the layings are by no means as concentrated as the parent locusts had been a month previously. The kind of place which is preferred by the adult locusts during the dry season and which combines with the gregarious behaviour of the locusts to cause concentration at that time is commonly not the same as the kind of place preferred by the laying females. Once the rains begin, the locusts can be seen to be moving off, not as a coherent swarm, but group by group, dispersing as they go. These facts throw greater emphasis on the importance of congregation of the adults in forming migratory swarms; as has been indicated before, however, egg-laying is nevertheless sometimes sufficiently concentrated to lead to formation of dense bands of young hoppers and the immediate formation of migrant swarms when the adults emerge.

Total Populations.

During the past few years, the North Rukwa Area has been the most consistently productive of dangerously large populations of the Red Locust and it has been repeatedly surveyed to assess the populations. A short summary of some of the results is shown in fig. 1. In 1954 and 1955, for many months it was not possible to assess the populations in the two easternmost sectors because of flooding. Accordingly, the lines in fig. 1 show the total estimated populations in the three other sectors, while the circles indicate populations for all five sectors, when those were estimated.

The figure shows that reasonable internal consistency has been achieved by the assessment methods used. Emigrant swarms were formed in 1954 and three actually emigrated; details of one of these swarms are given on p. 280. In 1955 and 1956, aircraft spraying had been adopted and although emigrant-type swarms formed, only one left the grasslands before being destroyed. It looks as if, in

this Area, total populations of 20 million do not form emigrant swarms (1953) but other data suggest that populations of 50 million do (August 1954). Further experience is required to narrow the gap, for prediction purposes.

Value of Population Assessments.

In early 1954, there were divergences of opinion about the importance of the young adult population in the North Rukwa. Of three experienced men, two considered that control could be withheld for several months but the other took a serious view of the immediate danger of emigration. A fourth man carried out a quantitative assessment of part of the Area, as a result of which all possible men, machines, and materials were rushed in to cope with a serious infestation; even so, a swarmlet of 5 to 10 million locusts got out two months later and was destroyed only after tremendous efforts. As early as 1954, the assessment technique had proved its value.

Again, in 1956, at the end of the hopper season, that part of the North Rukwa Area that could be traversed by Land Rover, or easily entered on foot, contained few locusts. Deeper incursions into the large flooded zones showed that there were a good many locusts in places but once again the opinions expressed were divergent. Fortunately the Swamp Skipper was available and was used for a systematic assessment (Table V). Nearly 1.500 counts of 0·1 mile were made

TABLE V.

Calculated results of locust population assessment of North Rukwa Outbreak Area, 28th April to 9th May 1956.

Locusts per 0·1 mile	Mean density per sq. yd.	Locusts (millions)	Acres (thousands)
0 ..	0	0	63
1—10 ..	0·02	3	37
11—100 ..	0·2	32	32
10^2—10^3 ..	1·3	179	29
$>10^3$ ..	7·7	69	2
	0·36	283	163

The figures are weighted for uneven sampling and are re-calculated from the supposed value of 1·6 yd. for the equivalent strip of the Swamp Skipper to a value of 1·2 yd. to facilitate comparison with Land Rover results in other Tables.

and the total population revealed was 283 million young adult locusts (c = 1·6 yd.), quite enough to produce a score or more of emigrant swarms. The data were, in this case, analysed in detail.

Assuming that the sampling was fair and adequate, not only for arriving at an average density, but also for showing the frequency distribution of densities, the acreages at various densities were calculated. In the absence of any large body of data, it was assumed that the population would have to be reduced to near the 1953 level at about 20 million to prevent emigration; to get as low as 35 million at once, the Table shows that over 30,000 acres of the denser locusts, averaging less than two per sq. yd., would have required clearing completely, for which the cost in concentrated contact insecticide alone would have exceeded £20,000. The alternative plan was to retain the hired aircraft, to await the spontaneous congregation of the locusts, and to spray only selected dense patches as they formed. This would economise insecticide, though it would cost more in

aircraft hire charges. The latter plan was adopted with the result that fewer than 4,000 acres were sprayed at an average density of 14 locusts per sq. yd. and the population was reduced to less than one per cent. of its original size. The development of the assessment method and the cost of the Swamp Skipper had been paid for in a single season.

Natural Mortality.*

In the three assessments of the total population of North Rukwa in 1953, the first in July and the last in October, far from there being evidence of natural mortality, the estimated population remained steady, although 10–15 per cent. of the locusts were killed by insecticides. There must have been some natural deaths, for example from predatory birds, but the assessment method was not refined enough to reveal them. It was felt at the time that one special feature of the outbreak areas might be that conditions there were specially favourable for survival of the adults during the long dry season, from April to November. Nevertheless, another species of locust in its outbreak area is not so fortunate: Smit (1939) records that the maximum length of life of adults of the Brown Locust is about 12 weeks; in four generations he found, however, a natural mortality of 44 (36–52) per cent. during a four-week period. Such a mortality in North Rukwa would surely have been detected in 1953.

In 1957, however, reductions of populations believed to be due to natural mortality were conspicuous in several outbreak areas of the Red Locust. In North Rukwa in May, scouting with the Swamp Skipper gave a total of 6·7 million locusts; by October (Land Rover), this was reduced to 2 millions, a drop of 70 per cent. without any use of insecticide. In Central Rukwa, from April to October, the total fell by 84 per cent. from 16 millions to 2·6 millions, again using the Swamp Skipper for the first estimate and a Land Rover for the second, and without any insecticide attack. One might suspect that figures obtained with the Swamp Skipper are not being correctly compared with those of the Land Rover, but in Iku Area in the same year, using a Land Rover with some scouting on foot on both occasions, the total dropped from 4·7 millions in mid-August to 0·5 million in October, a loss of nearly 90 per cent. Although proper figures cannot be given for the Mweru wa Ntipa Outbreak Area, a similar reduction was evident there, again without use of insecticide. With such low initial populations, swarm emigration can be excluded, and there is no evidence that emigration either by swarms or by individuals occurred, so that natural mortality is the probable explanation of the reductions in populations in all four areas.

As a result of such mortalities in all areas in the dry season of 1957, with minor insecticide attacks in the Malagarasi area, the total breeding population of all the outbreak areas together except Malagarasi for the season 1957–58 was probably under 7 millions, a figure worth comparing with the North Rukwa figures given in fig. 1; Malagarasi had about 12 million locusts.

A possible explanation for the differences between 1953 and 1957 is indicated by a correlation found by Mr. P. Symmons (unpublished, but see also Gunn, 1955, 1956), namely that a wet season of above average rainfall is followed over a year later by low adult populations, and *vice versa*. This correlation is probably explained by the water content of the soil in the following breeding season affecting the success of breeding; but it is also possible that heavy rains make unfavourable conditions for survival of adults in the immediately following dry season, so that the breeding stock is greatly reduced before egg-laying begins.

Now the rains of 1952–53 were poor and the apparent survival of adult locusts was high. The rains of 1956–57 were heavy and survival was poor. It is too early to find out whether multiplication from the surviving parents in 1957–58

* This section was added just before the paper went to press.

was high or low, but it is hoped to obtain evidence, for insecticides were used in only two outbreak areas. Soil moisture is being investigated and more frequent population assessments are intended in 1958, after a rainy season that has been very poor so far (February 1958). At present it looks as if Mr. Symmons's correlation may be due both to parental mortality and to poor multiplication of the survivors.

Summary.

A method is described of estimating the total numbers and frequency distributions of adults of the Red Locust, *Nomadacris septemfasciata* (Serv.), in outbreak areas of hundreds of square miles, based upon counting the numbers that fly up in a two-yard strip in front of a moving vehicle. The method has proved itself valuable for indicating both immediate and future requirements for killing the locusts, but it requires refining for some research purposes.

By this method, the importance has been clearly shown of the process of congregation of scattered adult locusts in forming emigrant swarms that could start a plague. The locusts do not congregate but actually disperse just before laying eggs.

The total population in part (189 sq. miles) of the North Rukwa Outbreak Area (a self-contained area of 253 sq. miles) in Tanganyika Territory has been followed for four years. There are indications that a small migrant swarm contains 5–10 million locusts, that a total population in the whole of the North Rukwa Outbreak Area of 20 million locusts is unlikely to yield a migrant swarm, but that 50 million locusts could readily do so.

In 1953, after poor rains, no natural mortality was detected between July and October by the assessment methods described. In 1957, after good rains, natural mortality of 70–90 per cent. was revealed by the same methods, although the dry season was not fully covered by the assessments.

Acknowledgements.

It is a pleasure to acknowledge with gratitude the information supplied by both the members of the Service and the visitors who are named in the text, and the discussions to which they have contributed. We also wish to thank Mrs. Barbara Gunn for her help to one of us in the field in 1952 and 1953, when the methods being tried at first seemed so unpromising.

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LABORATORY COLONISATION OF THE MOSQUITO, *ERETMAPODITES CHRYSOGASTER* GRAH.

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The virus of Rift Valley fever was isolated six times from mixed lots of wild-caught forest mosquitos in 1944 (Smithburn, Haddow & Gillett, 1948). Although several species were concerned, the circumstances of the isolations indicated that *Eretmapodites* spp. were the most important. Species of the group of *E. chrysogaster* Grah. were more numerous than any of the other species of *Eretmapodites* represented, and mosquitos of this group were later used in the successful laboratory transmission of Rift Valley fever virus from mouse to lamb, from mouse to mouse, from lamb to lamb and from lamb to mouse (Smithburn, Haddow & Lumsden, 1949). The mosquitos used in these transmission experiments were both wild-caught adults and adults reared from wild-caught larvae. In view of the possible importance of this species-group in the epidemiology of Rift Valley fever, and its ability to transmit the virus of yellow fever (Bauer, 1928), it was decided to attempt the laboratory colonisation of at least one of the species of the group. This paper describes the successful colonisation of *Eretmapodites chrysogaster, sensu stricto*. The account is given in some detail in view of the difficulty that is often encountered in attempts to colonise mosquitos.

Source Mosquitos.

Mosquitos of the *E. chrysogaster* group consist of ten known species (van Someren, 1949; Hopkins, 1952), ultimate separation of which depends on examination of the male genitalia. In order to start a colony of one of them, therefore, it was necessary to obtain batches of eggs from single isolated wild-caught females of the group, and to establish the identity of each female by subsequent examination of the male progeny. A similar method was used in the transmission experiment mentioned above (Smithburn, Haddow & Lumsden, 1949).

Females of the *E. chrysogaster* group were caught in Lunyo forest, near Entebbe, in March 1953. Each mosquito was fed and isolated in a small glass tube provided with moist absorbent paper for egg-laying (Gillett & others, 1950). The eggs comprising each batch were usually laid in small numbers at intervals over a period of 8–14 days after the blood-meal. The laying of a batch of eggs in this way after a single blood-meal has also been noted by Bauer (1928) and Haddow (1946). One female laid eggs after each of seven blood-meals during a period of 100 days in one of the small glass tubes.

Larvae obtained from one of the batches of eggs laid by a single female were transferred to an aluminium pot of water and fed on a mixture of powdered dog-biscuit and "Bemax". Larvae of this genus are facultative cannibals (Bauer, 1928; Haddow, 1946), and it was found necessary to sort the larvae according to size to minimise the loss of larvae.

Pupae were transferred to a wooden cage (c. 3′ 6″ × 3′ 6″ × 2′ 6″) with gauze top, front and back. Humidity was kept high by covering the front of the cage with an absorbent cloth, the lower border of which dipped into a tray of water.

Adults.

Identity.

After death, males derived from the original batch of eggs were sent to Mrs. E. C. C. van Someren in Nairobi for identification; without exception they were *E. chrysogaster, sensu stricto*.

Mating.

Both Bauer (1928) and Haddow (1946) noted that *E. chrysogaster, sensu lato*, mated freely in small cages. The adults derived from the pupae in the present observations, however, were not at first seen to mate, even though they were kept under daily observation. A small swarm of males would follow each female and make what appeared to be attempts to connect, but the females were apparently not receptive. Although raisins were present, some of the females died after a week and it was decided to allow them a blood-meal, even though mating had apparently not yet occurred.

Swarms of males would follow each female even to the source of the blood-meal, and some of them would settle beside the female as she fed. As soon as she had fed, mating occurred. This was observed very many times through several generations; mating did not occur until after the female had had her first blood-meal, the female usually accepting the male on her way from the host. Sometimes mating occurred on the host immediately the female had withdrawn her proboscis, and occasionally mating actually started while the female was still feeding.

Mating of *Eretmapodites* takes a long time, and has been described by Haddow (1946). He found that they would sometimes remain *in copula* for over an hour, but nine minutes was the longest observed in the present work. Once it had been found that mating occurred regularly after the blood-meal, no further difficulty was experienced with this aspect of colonisation.

Feeding.

Rabbits were tried as a source of blood, but were later discarded. Females of *E. chrysogaster* are very sluggish after a blood-meal and often remain on the host for some time afterwards. They are then easily killed by sudden movements, such as scratching, on the part of the host, males and females often suffering the same fate together. So many mosquitos were lost at this stage that it was found safer to feed them on human blood, the arm of the writer being placed in the cage for ten minutes, three times a week. Doubtless the difficulties could be easily overcome by immobilising the rabbit in some way, but it was found convenient to continue with the human host as it enabled observations to be made on the mating and feeding behaviour.

Oviposition.

Bauer (1928) and Haddow (1946) found no difficulty in obtaining eggs from this species group, and in the present work the original wild-caught females laid readily on the moist paper in the small glass tubes. It was decided, therefore, to provide trays of moist paper in the cage for egg-laying, but it was found that very few eggs were laid on these. Moist cotton-wool was substituted for the paper, but still exceedingly few eggs were laid. In fact, so few eggs were laid that, in order to maintain the new colony to the next generation, it was necessary to remove some of the gravid females to the small glass tubes. Within an hour or two eggs were laid on the moist paper at the bottom of the tubes. These eggs were used to start the second generation.

In view of the unexpected difficulty in obtaining eggs in the large cage, trials were made using oviposition containers of different sizes, including the small glass tubes used for the original eggs from the wild-caught females, until almost the

whole floor-space was covered. Some of the containers presented moist paper, others moist cotton-wool, and yet others presented free water over paper or cotton-wool. Again very few eggs were laid.

E. chrysogaster group larvae are often found in nature in the water held in the fallen bracts of the banana flower (*Musa* sp.). Some of these bracts were collected from banana trees, and were heat sterilised in order to kill the mites and other organisms which are frequently found on them. One of these boat-shaped sterilised bracts was then placed on the floor of the cage and partly filled with water. During the following 24 hours, very many eggs were laid, some of them on the surface of the water, others on the inside surface of the bract just above water level. No more difficulty was experienced with oviposition, and sterilised banana bracts were used successfully for over a year.

Larvae.

Banana bracts bearing eggs of *E. chrysogaster* were transferred to 1-litre aluminium pots of water. The larvae hatched and spent their early stages eating the banana bract. Gradually increasing amounts of powdered dog-biscuit and "Bemax" were added to the water daily. By the time the larvae had reached the third instar very little remained of the bract. Provided that small larvae were separated from larger larvae, and the number of larvae per pot was restricted to about 100, very little cannibalism occurred. It seems likely that the presence of the large bract in the water helped in reducing the amount of cannibalism by providing cover for the larvae. Many of the larvae spent much of the time almost buried in the tissues of the bract, while eating away its substance; some of these larvae were difficult to dislodge.

The colony flourished for over one year, when it was discarded owing to a change in the programme of work on Rift Valley fever virus.

Summary.

A colony of *Eretmapodites chrysogaster* Grah., *sensu stricto*, was maintained successfully for over a year without any reinforcement.

Identity of the mosquitos was established by starting the colony from a single batch of eggs laid by a single wild-caught female mosquito, and subsequent examination of the genitalia of the male progeny.

Mating occurred regularly after the first blood-meal of the female. In fact the females would not accept the males until they had started, or had finished, their first blood-meal.

Eggs were laid on the sterilised, water-filled bracts of banana flowers. Moist paper, moist cotton-wool or free water above paper or cotton-wool proved unsatisfactory as egg-laying media.

Larvae fed largely on the substance of the banana bracts on which the eggs had been laid. The banana bract also provided cover and so reduced the incidence of cannibalism among larvae.

Acknowledgement.

It is a special pleasure to thank Mrs. E. C. C. van Someren of the Division of Insect-borne Diseases, Medical Research Laboratories, Nairobi, Kenya, for kindly undertaking the examination of the males.

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PRELIMINARY NOTE ON THE BIOLOGY OF *GLOSSINA VANHOOFI* HENRARD.

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(Plate XII.)

Our observations were made in the Belgian Congo in the general region of Irangi, at the I.R.S.A.C. field station for forest studies, 150 km. on the road from Bukavu to Stanleyville and some 120 km. from Lwiro, the main I.R.S.A.C. research centre at 1°50′S. lat., 28°30′E. long. *Glossina vanhoofi* Henrard was first taken there in 1955 (van den Berghe & Lambrecht, 1956).

Irangi is situated in the narrow valley of the Luhoho river at an altitude of +900 metres in a dense natural rain-forest which, at this altitude, replaces the mountain-forest of the western slope of Mount Kahuzi (3,300 metres). It is difficult to place this forest in any particular type or class. However, *Gilbertiodendron dewevrei* is the most conspicuous big tree, together with *Staudtia* sp. One could call it a transition between the mountain-forest and the tropical lowland woods which, further to the west, cover the country on more gentle slopes towards the Congo river (Lualaba). The humidity in the forest at Irangi is very high and the trees are covered with numerous epiphytes. The annual rainfall is estimated to reach the 3,300 millimetre mark. The rainfall is less in June and July and sometimes during the month of January, but there is no well marked dry season when rainfall is nil. The region is rather thinly populated by natives of the Batembo tribe. Scattered villages are found on the more important trade paths winding through the forest and along the road to Stanleyville. The system of rivers is well developed, all flowing into the Congo Basin. Hundreds of smaller streams drain the water from as many valleys, the country being much broken and hilly. Some hills are several hundred metres above the valley floor. This hilly country slopes down and becomes almost flat as it reaches the Congo river, about 480 km. to the west.

At first, *Glossina vanhoofi* seemed very scarce, an odd one being caught from time to time by an occasional search party at the junction of the rivers Luhoho and Ilianga in a manioc field 2 km. from Irangi. An occasional fly was sometimes found in the forest and game reserve of I.R.S.A.C. on the right bank of the Luhoho river, and once in a light-trap intended to catch mosquitos. *G. palpalis fuscipes* Newst. was equally scarce, being found in very small numbers at different places along the Luhoho river. No human sleeping sickness has been reported as yet, as far as we know.

During the month of October 1956, a more thorough search was made in the I.R.S.A.C. forest reserve. Inspired by our experience with *G. brevipalpis* Newst. in the Mosso valley (van den Berghe & Lambrecht, 1954) and the description of the work done by Nash & Davey (1950) and Nash (1952) on the forest species, *G. medicorum* Aust., we looked for flies resting on tree trunks or other vegetation. The first example of *G. vanhoofi* was thus seen resting on the stem of a small sapling of a species of the Rubiaceae during the afternoon of 31st October. The fly was resting on the tree at about one metre above the

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forest floor, head down, and raised from the surface by the extended forelegs (Pl. XII, fig. 1). That same afternoon, eight more examples of *G. vanhoofi* were thus seen in a similar position. All of them were resting on small saplings. More flies were found during the days following, but often the search met with disappointingly few flies and was sometimes completely unsuccessful.

The study goes on, and it is hoped that the regular fly-rounds at chosen transects (see p. 295) will lead to more facts, not only of the biology of *G. vanhoofi* but of other species of forest *Glossina* as well. It is thought, however, that it may be useful to publish this first series of observations, as it may take a long while yet before a more complete picture can be obtained.

Observations on the Biology of *G. vanhoofi*.

Resting places.

It is, perhaps, not correct to use, in this particular case, the term resting place, which implies that the habitat is frequented by non-active flies. This may not be so. It is possible that further observations will lead to the discovery, later on, of more important and biologically more exact resting places. So far, all flies have been seen resting head down, as already described, at heights varying from 80 to 120 cm. above the ground. These first observations may be somewhat misleading owing to the fact that this is the height at which the eyes will usually wander when searching the trees. We instructed the fly-boys to keep a close watch at other levels, higher up or lower down, but, so far, only one fly has been seen above the usual height, at about 220 cm. All the flies were resting on small saplings of one or other of the following: a species of the Acanthaceae, a species of the Rubiaceae and *Gilbertiodendron* sp. (*Macrolobium*). It was observed that the bark of these trees was smooth and that no leaves hampered the view of the fly when resting at these places. The most favoured sapling is the one with a diameter not exceeding 2 or 3 cm. Very few flies were found on trees the diameter of which was more than 5 cm. No flies were found resting on a horizontal surface. The forest under observation (Pl. XII, fig. 2) is fairly open, with the canopy at about 30 or 35 m. The undergrowth consists of saplings of numerous forest species evenly spaced on an otherwise bare floor to which light only filters through. The most abundant component, however, of the lower storey seems to be the shrub, *Scaphopetalum* sp. The country is much broken and steep, where low hills alternate with equally abrupt valleys.

The main reason why it is thought that other resting places are still to be discovered is the fact that, so far, no fed flies have been caught. All flies rested head down and contained no blood. They were most probably hungry. In the laboratory it was observed, indeed, that most of the gorged flies rested head up. It is still a matter of supposition what places the fly may prefer at a certain time of the day or in relation to its hunger stage. It may well be that the fly is very sensitive to humidity and that its position is partly controlled by this factor. During daytime or according to the season and climatic conditions it may be supposed that the fly would adjust itself at a certain level and may rest even on the damp forest floor so as to protect itself from too rapid desiccation during very dry weather. Close examination of the forest floor and experiments with large nets thrown on the ground have, however, yielded no flies. Experiments are now under way, using platforms from which to examine the trees at a greater height up the trunks. This may possibly lead to the observation of a stratification due to a hunger stage effect or to climatic conditions.

Feeding habits.

As all flies so far captured have been in an advanced hunger stage it would seem logical to assume that we are dealing with a feeding-ground effect. The

small saplings favoured by *G. vanhoofi* give the fly a broader view than a much larger trunk, which would block off a very large proportion of the surroundings. Thus the fly is in a better position to observe, and this may also be the reason for its head-down position on the trunk.

A resting example of *G. vanhoofi* seems quite unconscious of movement around it or, at least, is not inclined to leave its resting place to investigate moving objects in its immediate neighbourhood. Thus it was easy to photograph, even on one occasion when it took a long while to change films in front of a fly. Unmoved by all the preparations and activities in front, it kept its position on the stem. Only the sudden lightning of the flash-bulb caused it to move off, shaken no doubt by the flash.

When one considers that, in the forest, the range of visibility is limited and light very poor it seems logical, indeed, that smell could act as a strong stimulus in forest flies. The olfactory stimulus could also explain the curious fact of one of the fly-boys coming back to camp who caught seven specimens of *G. vanhoofi* in 15 minutes when he had to stop on the main road to repair a tyre on his bicycle, when he was very hot and perspiring freely. The time was about four o'clock in the afternoon on a very sunny day. Strangely enough, a search of the same place, and also the river and forest in the vicinity, a number of times, did not produce flies. One day later, the same fly-boy caught two examples of *G. vanhoofi* while he was washing at a small stream. It has thus occurred to us that the fly may use open areas, above rivers or along roads, to travel in search of food when it is much pressed by certain circumstances of hunger. It is very rarely that man is attacked by *G. vanhoofi*.

A somewhat unusual set of circumstances, in which relatively more flies were caught, should be mentioned here. This first occurred at the start of our observations. There seemed to be a certain concentration of adults of *G. vanhoofi* in the immediate neighbourhood of an animal bait-trap used for the study of the attraction of the mosquitos of the Irangi forest. This simple trap consists of a mosquito-net tied to trees so that the lower edges are at about 40 cm. from the ground. In the space inside the net are placed a number of monkeys in small cages. The idea is that the mosquitos, attracted by the smell of the animals, will fly into the net and, later, try to escape by flying upwards, thus getting trapped by the ceiling of the contraption. Examples of *G. vanhoofi* were found from time to time in the trap, the highest number thus caught being four in a single day. It may be that more flies than these entered the trap but that, owing to its crudeness as a means of catching *Glossina*, a number of flies found their way back and out by the 40-cm. gap between the lower edges of the net and the forest floor.

It was thought that the relative concentration of fly around the mosquito-net might have been due to the smell of the bait animals. However, the large white surface of the mosquito-netting, very conspicuous at a good distance, might also have played a part. In order to find this out, an air-signal panel, one side glossy white, the other side brilliant orange, was hung in a tree on the slope of a hill in the Luhoho valley. So far, no particular attraction to this spot has been observed so that, after all, the stimulus of smell may be the important one. It should be noted that from outside the trap the animals themselves are not conspicuous. The monkeys, which are changed every day, are confined to narrow cages made of wood sticks which leave them without much mobility while the cages are mostly hidden under the mosquito-net so that there is very little chance to see the animals from the outside.

Natives tell of a definite concentration of flies at certain points whenever a herd of buffalo or elephant passes in the vicinity. We have not yet been able to check on this, but Jackson (1955) was unable to demonstrate it in the case of *G. morsitans* Westw. It seems possible, however, from what we observed

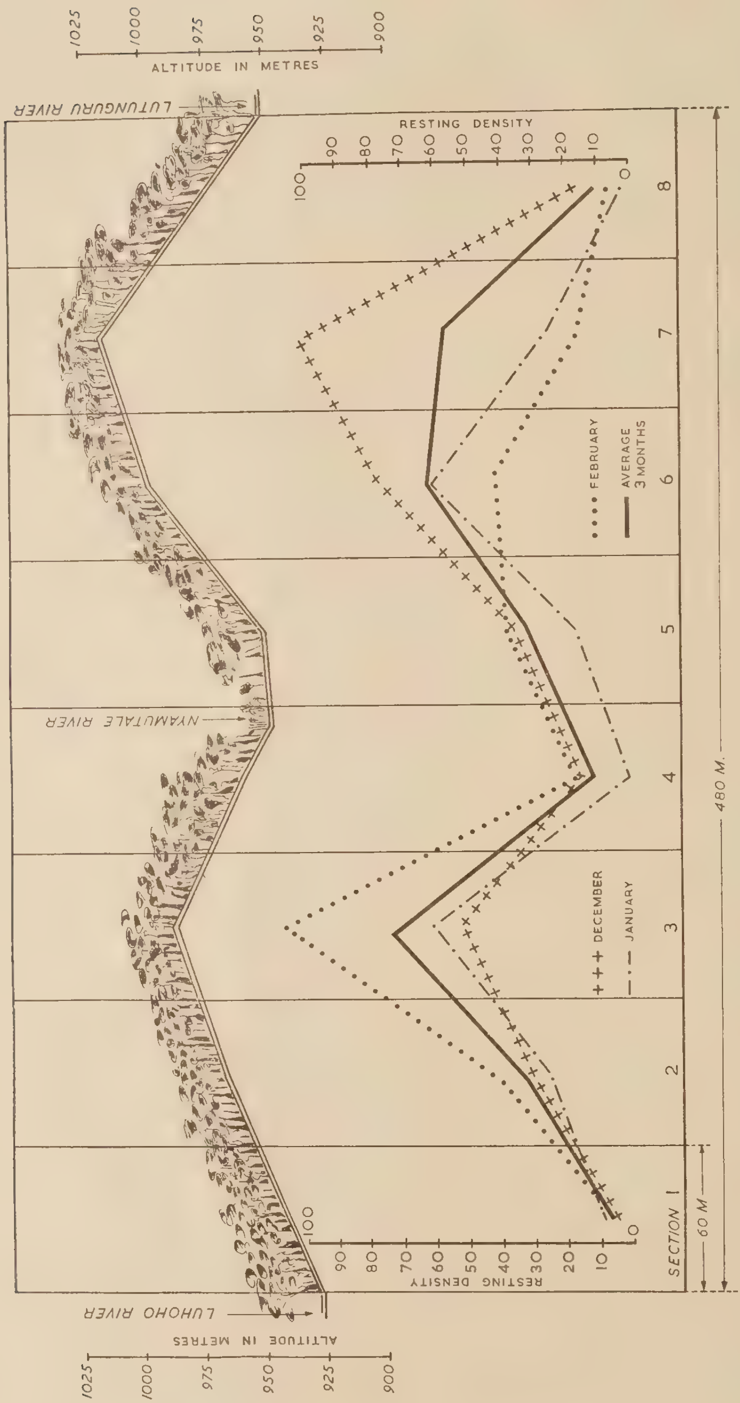

Fig. 1.—The monthly resting density of *G. vanhoofi* in each of eight sections in number-I transect, which sampled three valleys and two hills.

with the trap, that a herd of large animals would be very attractive to flies over a wide area and that at a certain point a concentration of hungry flies could result. It would be reasonable to expect that, a few days after the herd had passed, one might still find a number of flies lingering about at the concentration point, and that among them there might be a number of hungry flies that had been unable to get a feed or that had come too late to overtake the animals. These flies would eventually disperse, but before that they would be noticeable to people who happened to pass that way and who might even be attacked in the absence of the preferred host.

The population of a forest species of *Glossina* may be far more dispersed than a savannah one for many reasons. Host-animals may be spread over a large area, metabolism, and thus activity, may be slower and the immense expanse of the forest will give the fly an unlimited living space. Forest flies may wander for many miles without being in danger of leaving a favourable habitat. In such conditions it would be possible for a hungry fly to travel long distances before a favourable host is found and before it has had its feed.

Rearing in the laboratory.

So far no replete flies have been found and so it is impossible to tell what sort of blood the wild flies take.

Having two batches, each of about a dozen wild-caught flies, we tried to feed them on porcupines (*Atherurus africanus*) of which there were several in captivity at the Irangi research station at the time. The attempt was completely successful. Out of the 26 flies, only three died during the first week, and these may have been injured when caught. The others fed easily and greedily on the porcupines through the wire gauze of the Bruce boxes in which they were kept. Once fed, they seemed to like sitting head upwards, the abdomen was much distended, while a clear yellowish liquid was expelled in small droplets from the end of the abdomen. The boxes were kept on a tray containing some water to assure moisture, and were partly covered with a damp cloth to provide shade and coolness.

A number of larvae have been born in the laboratory at Lwiro, and have pupated normally. Emergence of the adult fly takes place after an average of about 35 days in an insectarium kept at 26°C. and 90 per cent. relative humidity.

Breeding sites.

Search-parties for pupae in the forest have been successful, but the number of living pupae found was very small in comparison with the empty puparia. Pupae were found in most of the "classical" breeding places, such as: under logs, low-inclined trees, over-hanging earth-banks of certain small streams and sometimes between aerial roots of certain species of trees. It is important to note that, though most of the time the soil, even in the sheltered situations of the breeding places, tends to be water-logged, it has a loose structure due to the lace-work of thousands of small roots, a fact which must facilitate, and is perhaps essential for, the emergence of the fly.

Fly Population and Distribution in the Forest.

In order to have a more precise picture of the population of *G. vanhoofi* in the forest of our Irangi research station, studies have been made on a number of transects. One of these, the number-I transect, will be described here in detail and all the information so far available will be summarised. The lay-out of this number-I transect was as follows. A path was measured, running eastwards from the Luhoho river and reaching the Lutunguru river after a distance of about 500 m. This path ran up over a hill, then down into the smaller but

TABLE I.

Number of flies and height (in cm.) at which they were seen or caught, per month and time of day, in each section of transect.

1. December and part of November (total number of visits, 85).

Section	Morning		Midday		Evening		Total number	Resting density
	No.	Av. ht.	No.	Av. ht.	No.	Av. ht.		
1	1	120	1	110	0	—	2	4
2	6	138	5	96	5	142	16	31
3	12	141	8	142	7	153	27	53
4	3	156	4	157	1	70	8	16
5	10	155	5	152	3	130	18	35
6	16	138	15	143	9	130	40	78
7	25	147	19	132	10	134	54	106
8	2	125	4	137	2	110	8	16
Total flies	75		61		37		173	
Weighted mean height ..		144		136		134		
Mean resting density ..								42

2. January (total number of visits, 58).

Section	Morning		Midday		Evening		Total number	Resting density
	No.	Av. ht.	No.	Av. ht.	No.	Av. ht.		
1	0	—	1	110	2	60	3	9
2	6	148	1	170	2	125	9	26
3	9	164	7	117	5	116	21	60
4	0	—	0	—	0	—	0	0
5	3	143	2	165	1	100	6	17
6	12	152	3	160	6	120	21	60
7	5	136	3	137	1	120	9	26
8	0	—	0	—	1	170	1	3
Total flies	35		17		18		70	
Weighted mean height ..		151		136		114		
Mean resting density ..								25

3. February (total number of visits, 67).

Section	Morning		Midday		Evening		Total number	Resting density
	No.	Av. ht.	No.	Av. ht.	No.	Av. ht.		
1	0	—	2	135	0	—	2	5
2	7	138	5	146	4	127	16	40
3	19	154	11	120	13	150	43	107
4	2	140	1	100	4	130	7	17
5	8	132	3	150	4	125	15	37
6	12	149	3	90	2	85	17	42
7	4	150	1	180	2	150	7	17
8	1	140	0	—	2	85	3	7
Total flies	53		26		31		110	
Weighted mean height ..		146		128		133		
Mean resting density ..								34

steep valley of the Nyamutale river, up a second hill and down again into the Lutunguru valley. Thus the path sampled three valley stations and two hill stations (see fig. 1). As no example of *G. vanhoofi* was ever caught attacking man in these circumstances, flies were sought in their resting places on vegetation. The path was divided in 60-metre sections, so that there were eight sections on the number-I transect, totalling 480 metres. Three fly-boys searched for flies along this path, on the vegetation bordering it. The transect was visited three times a day, in the morning from 0630 to 0830 hr., at midday between 1100 and 1300 and during late afternoon from 1530 till 1730 hr. This search was made on four days in the week, twice in the east-west direction, twice in the west-east direction. A record was kept for each visit and for each 60-metre section of the transect. The following data were recorded for each fly: height of the fly on the tree (whether captured or whether seen), the sex and the hunger stage (unfortunately only unfed flies have been seen, so far). Most of the caught flies were kept alive and brought back to the laboratory at Lwiro for further study. Some flies were marked and released in order to get information about their movement and range of flight.

The work was frequently hampered by rain. This, and the difficulty of finding the flies, were the main reasons why only 353 have been recorded during a three months' survey. The data collected, however, give some idea of the population of one species of forest fly.

TABLE II.

Summary (from Table I) of monthly totals of flies, by times of the day.

Number of flies caught or seen	Morning	Midday	Evening	Total	Visits
December	75	61	37	173	85
January	35	17	18	70	58
February	53	26	31	110	67
Total	163	104	86	353	210

Numbers of flies and resting height.

The monthly figures for numbers of flies seen or caught in each of the three daily searches, and the height at which they were resting in each of the eight sections are shown in Table I, and are summarised in Tables II and III. In all

TABLE III.

Summary (from Table I) of monthly mean resting heights (cm.), by times of the day.

	December	January	February	Mean of monthly mean values
Morning	144	151	146	147
Midday	136	136	128	133
Evening	134	114	133	127
Weighted means ..	139	138	138	

three months, the highest catches were in the morning, and in two of them (January and February) there was little difference between midday and evening catches. In all three months, the flies rested nearer to the forest floor later in the day than they did in the early morning. This could be an adjustment to balance the increased evaporation rate of the air later in the day.

Sex ratio, mean average resting height and resting density.

Some of the data from which Table I was derived are set out in a different form in Table IV, the 3-monthly totals of the sexes in each section being shown separately. Flies shown under "Sex not determined" are those that were observed on a tree but which escaped capture. The sex ratio in the 3-monthly period is shown to have been near to 1:1 in the various sections and to have been almost exactly 1:1 for all sections combined. The monthly totals for each sex for all sections combined is shown in Table V and here also the ratio was,

TABLE IV.

Numbers of males and females, total numbers and resting densities for three months of survey (detailed by sections).

Section	Male	Female	Sex not determined	Total	Resting density
1	0	4	3	7	6
2	16	18	7	41	33
3	35	39	17	91	72
4	6	7	2	15	12
5	15	19	5	39	31
6	35	26	17	78	62
7	23	20	27	70	56
8	3	2	7	12	10
Total	133	135	85	353	
Mean resting density					35

in every month, very near to 1:1. When the numbers of males and females are set out separately, and divided, monthly, into morning, midday and evening catches (Table VI), it is apparent that there was no difference in the sex ratio as between times of day or different months. In as far as the forest at Irangi is concerned, the population of *G. vanhoofi* seems to be very homogeneous in sex distribution as far as can be ascertained from catches in what are here called "resting places". The resting height appeared to vary in much the same way in all sections. On the other hand, Table III suggests that there is a difference in height between morning, midday and evening captures. When the figures for resting height are examined separately for the two sexes, it is found that the mean average heights over the three months showed a slight difference between the sexes, although this difference was not consistent from month to month (Table V).

As a measure of the fly population during each month, a figure, termed the resting density, has been calculated from the total numbers of flies observed

during the month, regardless of sex or age, per 10,000 metres of path. This differs from the "apparent density" of previous authors, which is defined as the number of non-teneral males caught per 10,000 yards of path (Jackson, 1953, p. 80). The resting density was calculated for each section separately,

TABLE V.

Numbers of males and females, total numbers (all sections combined), and average heights for each sex.

Month	Male	Av. ht.	Female	Av. ht.	Sex not determined	Av. ht.	Total flies	Mean average heights
December	58	138	57	137	58	142	173	139
January ..	26	141	28	129	16	150	70	138
February ..	49	142	50	133	11	143	110	138
Mean height		140		134		143		
Total flies	133		135		85		353	

the distance traversed per month in each section being arrived at by multiplying the length of the section by the number of visits per month, which are shown in Table I. The resting density in each section in each month is shown in Table I, and for the whole period in Table IV. These are also shown graphically in fig. 1,

TABLE VI.

Numbers of males and females and total flies (all sections combined), per month and time of day.

		December	January	February	Total
Morning ..	Male	25	13	24	62
	Female	23	12	24	59
	Sex not determined	27	10	5	42
	Total	75	35	53	*163*
Midday ..	Male	18	6	12	36
	Female	19	7	12	38
	Sex not determined	24	4	2	30
	Total	61	17	26	*104*
Evening ..	Male	15	7	13	35
	Female	15	9	14	38
	Sex not determined	7	2	4	13
	Total	37	18	31	*86*
Grand total					*353*

from which it is evident that there is a close correlation between the resting density and the profile of the transect, an increase in resting density being associated with the hill-tops. This could point to a negative reaction towards high humidity, the deeply enclosed valleys retaining a very high humidity for a good part of the day. Could it be that here is an example of a humidity relationship which is the reverse of that shown by species of *Glossina* that inhabit the savannah? *G. morsitans* is forced, by hunger, to abandon its relatively cool and humid habitat in order to search for food at the feeding grounds which are usually climatically very unfavourable, being hotter and much drier. Can it be that the forest species, *G. vanhoofi*, has to abandon its relatively drier perches up in the trees in order to search for food at the lower and much more nearly saturated levels near the forest floor?

Summary.

Glossina vanhoofi Henrard has been found at the I.R.S.A.C. field station at Irangi in the Belgian Congo in dense rain-forest. The fly does not normally attack man and was collected only by looking for it in its resting places. The fly rests on small saplings, head down, at an average height of about 133 cm. A three-months' survey on a fly-round transecting three valleys and two hill-tops showed that the resting density (defined as the total number of resting flies observed per 10,000 metres of path) was correlated with the profile of the transect, the hill-tops yielding more flies than the valleys. The fly-round was worked three times a day and showed the highest density during early morning in all three months; in two of them there was little difference between midday and evening catches. The resting height varied in much the same way in all the sections of the fly-round and the average height remained virtually constant during the three months of the survey. There was a slight difference between the sexes as regards average resting height, the females perching somewhat lower than the males. The sex ratio of about 1:1 was very constant throughout the day and the period of the observations.

There is some evidence which seems to indicate that this species is strongly attracted to possible host-animals by a sense of smell.

Puparia have been found in "classical" sites, but the proportion containing living pupae was small. The duration of the pupal period is about 35 days under laboratory conditions at 26°C. and 90 per cent. relative humidity.

G. vanhoofi in captivity feeds readily on the porcupine, *Atherurus africanus*.

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FIG. 1. An example of *G. vanhoofi* resting on a sapling in the forest at Irangi, 31.x.1957.

FIG. 2. View inside Irangi forest. Small saplings underneath *Ficus* tree. In foreground at left can be seen instruments and the lower part of a scaffold which supports an observation platform.

A NEW EUROPEAN SPECIES OF *PACHYNEMATUS* KONOW (HYMENOPTERA, TENTHREDINIDAE) FEEDING ON SPRUCE (*PICEA*).

By Robert B. Benson.

Dr. W. Thalenhorst, of the Niedersächsische Forstliche Versuchsanstalt, Göttingen, Germany, sent me some time ago specimens of what he took to be an abnormally dark form of *Pachynematus montanus* (Zaddach). These had been reared in 1952 from larvae, not at the time distinguished from the larvae of that species and found feeding with them on spruce (*Picea abies*) in the Harz Mountains in the previous year. Unfortunately the female was smashed in the post and I did not like to describe a new species that would have to be based on only a few males, though I was not able to identify them with any known species. In 1955, however, he reared another female of the same species and from this he tried to obtain eggs but without any success. This female I now have before me. No further specimens have been found.

Pachynematus styx, sp. n.

♀. Yellowish brown with the following parts black: antenna, head above antenna (except for the inter-antennal furrow, the narrow front and the broad hind orbits and the adjoining temples), the head behind, the thorax (except for the lateral lobes of the pronotum and the tegulae), the bases of the coxae, the femora above in part especially the hind pair, the hind tibia apically and in part above, the hind tarsus and the middle tarsus apically, the abdomen above and the apex of the sawsheath. Wings hyaline; stigma and venation brownish white, piceous on M. of forewing.

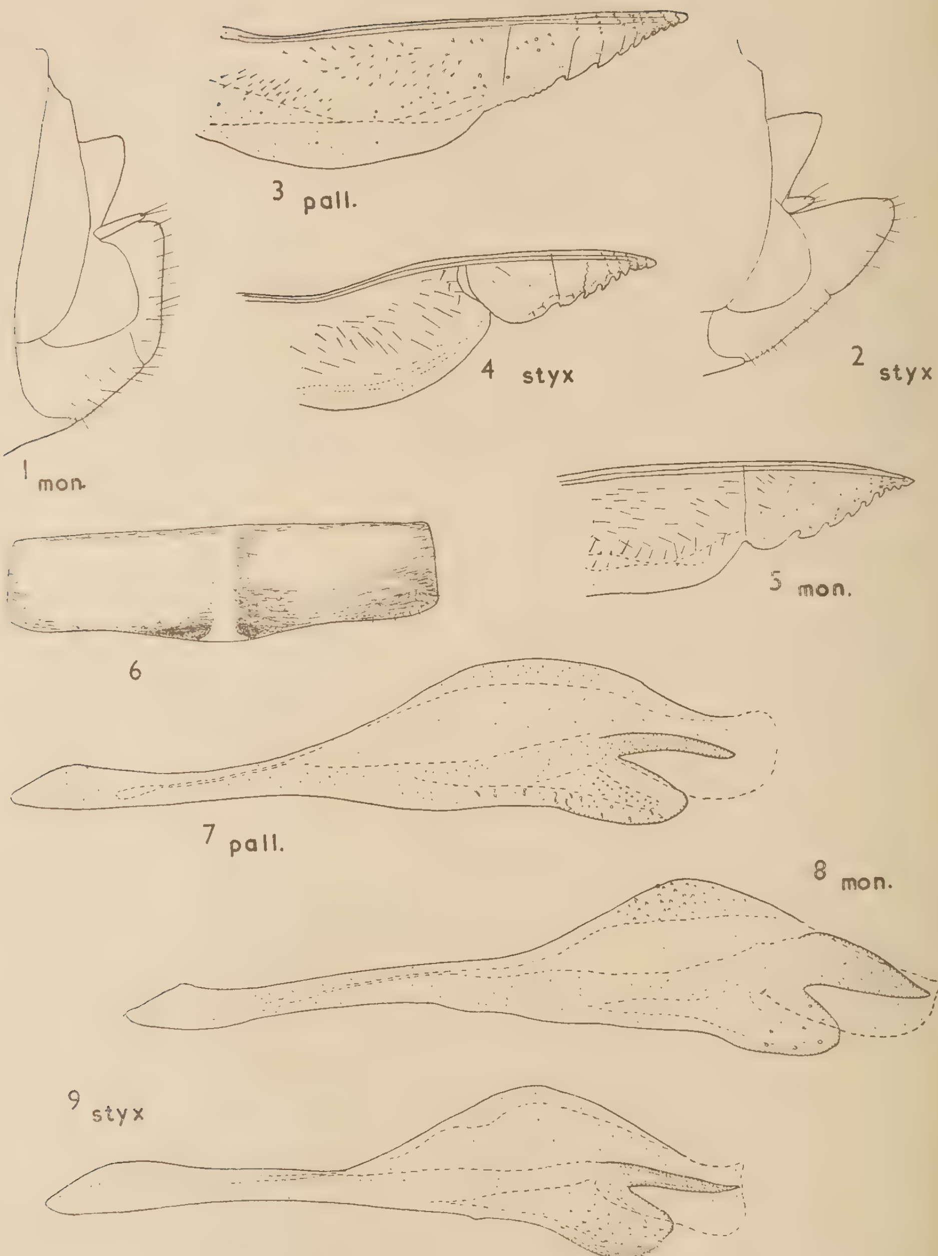
Head contracted slightly behind the eyes and with slight microsculpture especially on lower inner orbits but becoming obsolescent on frontal area. Antenna as long as stigma + C of forewing; 3rd, 4th and 5th segments almost equal in length; 3rd about $1\frac{1}{2}$ times as long as length of eye. Malar space about equal to distance between antennal sockets. Eyes large so that in lateral view they appear twice as long in the middle as the length of the head behind them; length of eye to height as 1·0 : 1·4. Frontal area in the form of a raised platform with a slight anterior wall not notched medially. Distance between the hind ocelli (POL) less than twice the distance from an ocellus to the hind margin of the head (1·0 : 0·59), and POL : OOL as 1·0 : 0·82.

Thorax shining between scattered microsculpture; medial furrow of mesonotum obsolete behind; scutellum flat and together with its post-tergite longer than broad (as 1·1 : 1·0). Legs with hind tibia slightly longer than femur + trochanters; hind tarsus a little shorter than tibia (0·9 : 1·0); basitarsus little longer than two following segments together; inner hind tibial spur a little longer than apical breadth of tibia and less than $\frac{1}{2}$ as long as basitarsus (0·4 : 1·0).

Abdomen transversely alutaceous above. Ovipositor short (about as long as hind basitarsus + $\frac{1}{2}$ following tarsal segment); sawsheath about $\frac{2}{3}$ as long as basal plate and acute in lateral view (fig. 2). Cerci very short. Saw (fig. 4) very like that of *P. montanus* (fig. 5). [It should be noted that the basal transverse band in the saw shown in fig. 4 is probably abnormal.]

Length 5 mm.

♂ as ♀ except that the legs are paler, having no black on the femora or tibiae and only on the apex of the hind tarsus, that the antenna is about as long



Figs. 1–2.—Sawsheath and basal plate in lateral view of: (1) *Pachynematus montanus*; (2) *P. styx*, sp.n.
Figs. 3–5.—Saw of: (3) *P. pallescens*; (4) *P. styx*, sp. n.; (5) *P. montanus*.
Fig. 6.—Apical tergite of *P. styx*, sp.n. ♂.
Figs. 7–9.—Penis valve of: (7) *P. pallescens*; (8) *P montanus*; (9) *P. styx*, sp. n.

as a forewing, that the inner hind tibial spur is about ½ as long as the basitarsus, and in the sexual characters. Apical tergite with but slightly developed armature (fig. 6); hypopygium narrowed to a rounded apex; penis valve as in fig. 9.

Length 5 mm.

GERMANY: South Lower Saxony, Sieber (Harz), c. 600 m., 1 ♀ (type) reared 1955 from larva collected vii.1954 on *Picea abies*, and 3 ♂♂ reared 1952 from larvae collected vii.1951 (*W. Thalenhorst*). (In British Museum (Natural History).)

The new species belongs to the small species-group of spruce-feeding sawflies previously consisting only of *P. montanus* (Zaddach) and *P. pallescens* (Hartig). In these the male has a slightly modified apical tergite and the female ovipositor is laterally compressed, but the saw is so reduced that it is only about as long as the hind basitarsus or half as long as the hind femur. From *P. montanus* and *P. pallescens* it differs in the acute profile of its sawsheath (*cf.* figs. 1–2), the saw (*cf.* figs. 3, 4 & 5), the shorter tibial spurs, the entirely black underthorax and the form of the penis-valve (*cf.* figs. 7, 8 & 9).

I have not treated these three species as belonging to *Pikonema* Ross (1938) as I do not regard this as a genus distinct from *Pachynematus*. But for those who do, it would surely be better to include these three species as complying more closely with the definition of *Pikonema* than with the typical *extensicornis* (Norton)–*clitellatus* (Lepeletier) group of *Pachynematus*. Then also would have to be included *P. scutellatus* (Hartig) and *P. insignis* (Hartig), together with *P. nigriceps* (Hartig), *P. leucopodius* (Hartig) and *P. imperfectus* (Zaddach) (all attached to *Picea* except *P. imperfectus*, which is on larch (*Larix*)).

The original references to these species can be found in Dalla Torre (1894). They were further dealt with by Enslin (1912–18) and those occurring in Britain by Benson (1951–58).

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* Pt. 2c in press, June 1958.

THE INITIAL STAGE OF MIGRATION IN SALT-MARSH MOSQUITOS.

By Erik Tetens Nielsen
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(Plates XIII & XIV.)

When my wife and I went to the United States in 1948 to study migrations of butterflies, Dr. Uvarov, Director of the Anti-Locust Research Centre, London, advised us to focus our attention on the very beginning of the migration. It is essential to understand the factors which release the initial phases of this behaviour in order to acquire an insight into the mechanism of the migratory habit.

In our observations on the migratory butterfly, *Ascia monuste* (L.), we always kept this advice in mind and found it eminently useful. The first part of this work has been published (Nielsen & Nielsen, 1950), and another more extensive report on the work, supplemented with quite recent additional observations, is under preparation and will soon appear.

This much might here be anticipated as a brief summary:

(1) The migratory activity is limited to a certain age of the adult butterfly so that a butterfly will not normally start on migration until it is 15–20 hours old nor will it start after it has become sexually mature, which occurs when it is about 30 hours old.

(2) The migratory activity is limited to a certain part of the 24 hours so that a butterfly will not normally start on migration before about 0900 hr. nor will it start after about 1400 hr.

(3) When the migrations start in the morning at 0900 hr., a large number of individuals will during the night have attained the age at which they are able to migrate and there is therefore a marked mass departure from the breeding ground at this time.

(4) The emergence is not evenly distributed over the 24 hours, but most of the adults appear in the middle of the day; this will tend to increase the number of butterflies which take part in the initial mass departure.

(5) After the first departure in the morning, there will for some hours be a smaller number of butterflies starting on migration, presumably individuals that emerged the preceding afternoon or early evening which are too young to start at 0900 hr. and which eventually attain the necessary adult age.

(6) Some individuals, having emerged around midnight, will be too young to start during the first daytime period of migration, and too old the following morning; such individuals will therefore not migrate at all.

It was further found that females had copulated before the migration, although the ovaries are still immature at that time, and that both sexes had fed before the take-off. Before and during the start of the migration there is in the outbreak area an enormous " milling around ", to use Fernald's expression (Fernald, 1937), sometimes with short flights in any direction, sometimes like clouds or snow drifting with the wind. The final direction of the flight is usually adopted by flying from flower to flower feeding at longer and longer intervals until finally the characteristic, determined migratory flight is adopted by one individual after another in a direction which, at least often, reflects the direction along which the feeding flight took place.

Observations in Fort Pierce.

With this knowledge of the butterflies, we turned in 1951 to studying the salt-marsh mosquitos migrating from the same marshes in which the butterflies are reared, the food-plant for the caterpillar being *Batis* from open marsh or from the black mangrove areas on the coast of Florida. In a recent work, Provost (1952) distinguished two forms of dispersion, by appetential and non-appetential flight, respectively, and stated that it was his belief that insect migrations are examples of non-appetential flight. The present work is concerned only with the latter, which may be defined as non-purposive spontaneous flight, the direction of which may be deflected by meteorological or topographical influences.

Dr. Uvarov's advice to study the initial phases of the migration especially is to some degree a necessity in the case of mosquitos. The smaller size of these insects and their nocturnal migrations make it necessary to use complicated and indirect methods, such as trapping, to study the actual migrations. It should, however, be possible to get some information on the beginning of the migration by direct observation, especially to see if the start of the migration is limited to a certain age and to certain external conditions as was found in *Ascia*.

Our earlier observations have been published (Nielsen & Nielsen, 1953); they dealt mostly with the general behaviour of *Aëdes taeniorhynchus* (Wied.) and the swarming of the males. Pertinent to the question of the start of migration were only some field experiments in which the mosquitos were marked by dusting with an aniline dye mixed with flour, a method developed by Clarke (1937). From direct observation we had learned that the number of newly emerged mosquitos increased during the day and that they stayed in the low vegetation close to the place of emergence; they could be forced to fly up for a short while by disturbing them. Shortly before sunset a more pronounced spontaneous activity occurred. The mosquitos were then moving rather inconspicuously up to the foliage of the higher vegetation. The following day there would again be large numbers of mosquitos in the grass. Marking was undertaken to find out if the mosquitos in the grass were newly emerged or whether old ones returned from overnight places in the higher foliage. We found that if all mosquitos were marked half an hour before sunset, only 15–25 per cent. of those present in the low vegetation next day would have been marked; two days after the marking, only one of 48 had been marked, and out of 458 mosquitos caught on the following days none had been marked. It was thus found highly probable that migration takes place at night and when the mosquitos are less than two days old—possibly at an adult age of 12–24 hours.

The fact that the disappearance actually represents a migration was shown by an experiment with radioactive individuals of *A. taeniorhynchus* (Provost, 1952). More than 300 marked individuals were recaptured and it seems that most of the females had migrated 8 to 20 km. from the release point.

During the latter experiment, the newly emerged mosquitos were kept, until release, in boxes with walls and roofs of screen wire. It was observed that during the increased activity at sunset the insects tried very strongly to escape and many males succeeded in squeezing themselves out through the netting. A similar observation was made in a large box (3 × 3 × 3 m.) built at the Archbold Biological Station for observations on the habits of these mosquitos under controlled climatic conditions. The roof was made of screen wire, and it was found that newly emerged mosquitos vanished from the cage, most likely through the roof.

Although we had good reason to believe that migration takes place in the active (nocturnal) period by individuals of a certain age, we felt that we should make a direct observation of the start of the migration and also that we needed better insight into the duration of the passive period before the migration.

During the emergence of an isolated brood in February 1952, we had a good

opportunity to observe the behaviour of newly emerged mosquitos in the same area at Fort Pierce, Florida, which has been described previously (Nielsen & Nielsen, 1953). The following observations were made on or adjacent to a narrow road in the innermost part of the mangrove swamp close to the hammock zone (the dense growth of hardwood and other subtropical trees and bushes), the mangrove here being 2–3 m. high. The breeding took place in pools on the road or in the mangrove close to it. *A. sollicitans* (Wlk.) emerged on 10th–12th February, and *A. taeniorhynchus*, in much larger numbers, emerged on 11th–18th February.

In the afternoon of 13th February we observed clouds of mosquitos everywhere in the grass along the road. At sunset (1813 hr.) the temperature was 20°C.; one-tenth of the sky was covered by alto-stratus clouds. There was no wind on the road, but the tree tops were moved by a wind from E. or NE., estimated to be 1–1·5 m./sec. At higher altitudes there must have been a very strong wind from the west as the vapour trail from a high-flying aircraft drifted from the zenith far to the east in about 15 minutes.

Towards sunset the resting mosquitos became active, and between 1810 and 1820 hr. a large number moved up on the mangrove leaves to about one and a half metres from the ground. At 1823 hr., a few were seen on the top leaves, and small clouds of mosquitos then started to fly up in the air. Until 1833 hr. such "puffs" continued to fly off, one to three times each minute, and, in between, many single individuals flew away. The direction of the take-off was 30°–60° upwards and towards the north. After the departures had stopped there were still many mosquitos in the vegetation. These departures were first seen by my wife, and none of us had the slightest doubt that here, for the first time, we were observing the actual departure for migration.

On the following evening, departures were again observed but in much smaller numbers. The wind was a little stronger, from NE., and the mosquitos followed the wind. On 15th February the number of departing migrants was again smaller. From 16th to 19th February the emergence was mostly from pools in higher and denser mangrove a little away from the road and observations were very difficult to make.

Determination of Age of the newly emerged Mosquitos.

In order to narrow the age limits at departure we tried to use the rotation of the hypopygium as an age indicator in young males. As is well known, the tip of the male abdomen, including the eighth segment and the external genitalia, is rotated through 180° during the earliest part of adult life. Roth (1948, pp. 282–284) found that in *A. aegypti* (L.) this process usually started one to four hours after emergence and was often completed in 15 to 19 hours. There was, however, considerable individual variation.

In *A. taeniorhynchus* we have found very nearly the same situation. Individual variation in this species is also too pronounced to permit a definite age determination of single individuals, but there can hardly be any doubt that for a *group* of individuals the rotation stage tells something about the average age of the individuals. It seems natural to operate with three or four stages of rotation: MI are males with less than 45° rotation, MIIa with rotation between 45° and 90°, MIIb with rotation between 90° and 135° and MIII with rotation 135° to 180°. In many individuals with rotation close to 90° it is difficult to decide whether they are just over or just below 90°. Therefore, for routine examination, much time is saved by using only three stages: MI for individuals with rotation not clearly started (Pl. XIII, fig. 2), MII for the clearly intermediate stages (Pl. XIII, figs. 1 & 3), and MIII for stages with rotation nearly or completely finished (Pl. XIII, fig. 4). Eighty eight males kept at room

temperature gave the percentage occurrence of the stages in relation to age shown in Table I. Based on these figures we have drawn the reference curves in fig. 1. It is clear that a group of which a large majority is MI is not older than 6–7 hours, and if all, or nearly all, have completed rotation they are more than 18–21 hours old.

TABLE I.

Percentage distribution of stages of hypopygial rotation in *Aëdes taeniorhynchus* in relation to age.

Hours after emergence	MI	MIIa	MIIb	MIII
0– 3	100	0	0	0
3– 6	95	5	0	0
6– 9	45	54	1	0
9–12	6	65	24	5
12–15	0	21	35	44
15–18	0	4	27	69
18–21	0	5	11	84
21–24	0	3	0	97

We felt that it would be useful to get an idea of the accuracy of the method and especially to be sure that the estimate of the stages of rotation was not subjectively influenced. This could be done by having two persons to make estimates of the same material independent of one another. Mrs. Nina Branch, of the Entomological Research Center, who has an unusually wide experience in the analysis of mosquito samples, was kind enough to examine 200 specimens from each of the samples collected in Tampa on 31st March 1953 (see below). The result of the independent estimates is given in Table II.

For the following paragraphs it is necessary to bear in mind that emergences are concentrated in a certain part of the day. This has been known for a long

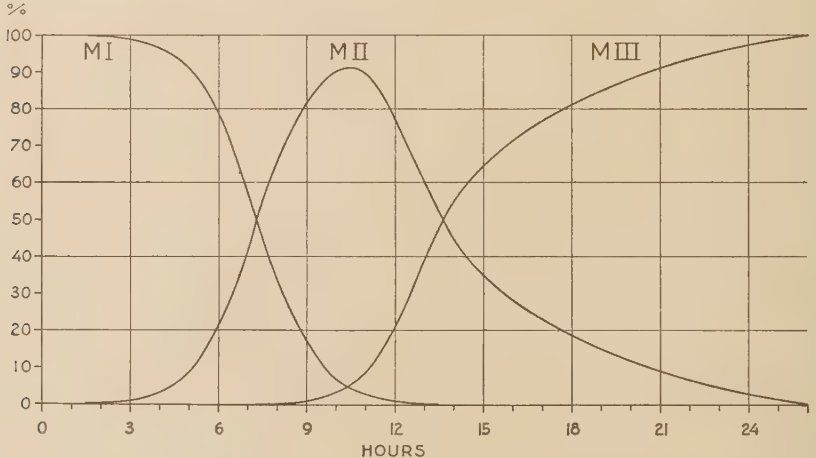

Fig. 1.—Percentage proportions of the stages of hypopygial rotation in *Aëdes taeniorhynchus* in relation to time after emergence.

time, de Réaumur (p. 610) already knew that "les cousins" appeared mostly around noon. From our own observations we knew that the emergence is concentrated around a certain part of the day, but we were puzzled about these peaks occurring at different hours in different broods. This difference became understandable later (Nielsen & Haeger, 1954) when it was learned that pupation

TABLE II.

Estimates, by two independent observers, of rotational stage of hypopygium in *Aëdes taeniorhynchus*.

Hour of sampling	MI as percentage of total*		Average age according to reference curve (fig. 1)	
	E.T.N.	N.B.	E.T.N.	N.B.
1600 hr.	65	70	$6^h40'$	$6^h20'$
1840 hr.	24	27	$8^h25'$	$8^h20'$
Migrants	24	24	$8^h40'$	$8^h40'$
1915 hr.	80	80	$5^h55'$	$5^h55'$

* Only one example of MIII was found among the more than 2,500 specimens included in this material. The figures in these columns are, therefore, arrived at from $\frac{\text{MI}}{\text{MI} + \text{MII}} \times 100$.

has a definite maximum at dusk while the duration of the pupal stage varies only with temperature, so that the peak of emergence can occur any time of the day according to the temperature at which the pupae develop.

From the large number of records of emergences in the laboratory (Nielsen & Haeger, 1954), a percentage distribution of emergence over the 24 hours has been calculated and is given in Table III.

TABLE III.

Distribution of emergences of *Aëdes taeniorhynchus* over the 24-hour period when the peak of emergences is between 0900 and 1200 hr.

3-hour periods	Emergences (%)	
	Found	Approximate values used in calculations
00–0300	0·7	1
0300–0600	3·1	3
0600–0900	12·7	13
0900–1200	59·0	60
1200–1500	21·8	20
1500–1800	0·6	1
1800–2100	1·8	1

The male mosquitos resting in the grass were sampled several times, and it was found that at 1300 hr. the proportion MI : MII : MIII was 94 : 6 : 0, in other words their average age was 4–5 hours, and the main emergence had evidently taken place between 0800 and 0900 hr. At 1800 hr. the proportion was 39 : 51 : 10, which is fairly consistent with the main emergence having occurred about 0700 to 1100 hr.

On all three evenings, when it was possible, we tried to catch the departing migrants. Of 103 males caught, one was undoubtedly MI, and another, somewhat damaged, possibly MI; 61 individuals were MII, and 40 MIII. This corresponds to an age of about 12–13 hours. It was mentioned above (p. 307) that a rather large proportion of the mosquitos remained after the departure; these might have been too young to migrate at that time. Based on these observations it seems reasonable to conclude that migration starts when individuals are 7–13 hours old.

When we have a thorough knowledge of the three factors: (1) distribution of emergences in relation to sunset; (2) time factor in hypopygial rotation; and (3) age of departure, it should be possible to determine one of these factors if the other two are known.

As the onset of departure occurs only after sunset, it seems likely that we have here a phenomenon similar to that known in *Ascia*—that there is a maximum number of migrants departing at the onset of the active period because during the preceding period a number of individuals has reached the age for migration and these have accumulated while awaiting the certain permissive part of the day, probably dependent, in the case of mosquitos, on the conditions of light (and possibly also of temperature). Just as it was observed that later in the day a smaller number of butterflies leave, one by one, as they eventually attain the necessary age to take off, it would be expected that mosquitos that had emerged later in the day would eventually take off after the maximum departure. This has since been shown to be the case (Haeger & Provost, in preparation).

As for the age of the females—it might be possible to determine it by means of the stage of development of the ovaries, a method found most useful in the butterflies. A number of departing females was caught and fixed in Bouin's Fluid (15 parts saturated aqueous solution of picric acid, 5 parts formol, 1 part acetic acid) and kept in 70 per cent. alcohol. After imbedding in paraffin, the abdomens were sectioned on the long axis, stained with hematoxylin-eosin, and mounted in Canada balsam. In all 21 females examined, the ovaries were found to be immature; none of them had mated—as was clearly seen from the empty spermatheca. The spermatheca of a non-migrating female is shown in Plate XIV, which indicates how easy it is to tell whether mating has taken place. Haeger (in preparation) later obtained further information on feeding and mating before departure.

During the first part of this investigation (Nielsen & Nielsen, 1953) the impression was gained that there was no difference in the times of emergence of the two sexes, but during the observations reported here we found this to be wrong. The percentage of females in samples of resting mosquitos on consecutive days in February was: 12th, 5; 13th, 19; 14th, 50; and 15th, 83. This corresponds very well with later findings in laboratory experiments (Nielsen & Haeger, 1954).

Observations in Tampa.

Another direct observation of the departure of migrating mosquitos was made in the following year.

A heavy fall of rain on 23rd March 1953 hatched a large number of mosquito eggs in the Tampa area. Observations were made west of the town at Rocky Point, south of the causeway. It was a mixed brood of *Aëdes sollicitans* and *A. taeniorhynchus*.

The first adults were seen on 29th March. The next day there were only a few, which disappeared slowly from the grass after sunset, and at 2330 hr. not a single one could be found. On 31st March there were already many mosquitos

in the grass at 0830 hr. but the main emergence seemed to be between 1130 and 1600 hr.

At sunset (1847 hr.) the temperature was 21°C. One-tenth of the sky was covered with cirrus and the wind was from SSW. decreasing from about 1·5 m./sec. to 0·5 m./sec. The relative humidity at sunset was 73 per cent.

The grass was teeming with mosquitos, practically all *A. taeniorhynchus*, and from 1815 hr. onwards the individuals stirred up as a result of our walking through the grass did not return or fly around, but took off, with the wind, toward ENE. at an angle of 30–45° to the horizontal plane. These provoked flights had some similarity to the provoked swarms observed in *A. cantans* (Mg.) (Nielsen & Greve, 1950) and *A. caspius* (Pall.) (Nielsen & Nielsen, in preparation).

The spontaneous departure of the migrants lasted from 1859 to 1914 hr. and was very spectacular. It was like a rain shower coming up from the grass; it could be felt on the hands and in the face when the migrants hit the observer.

The best observation post was 5–10 m. downwind, where the mosquitos came up against the western sky as background and most of them passed in front of and over the head of the observer.

The following evening there was a similar but much smaller departure, from 1859 to 1910 hr. Many of the migrants moved up to the top of nearby bushes (especially *Baccharis*) and took off from there.

The emergence continued on the following days, and there was a definite departure every evening.

During the observations of 31st March, samples of the resting population were taken at 1600, 1840, 1915 (before and after initiation of migration), and at 2200 hr. The last comprised only 120 individuals; there were very few to be found at that hour. The other samples were very much larger, and so also was a sample of the departing migrants.

As the numbers this day were so much larger than on the preceding days and as most of the older ones had departed, the expectation was that few older mosquitos would be present to obscure the picture. As far as the males were concerned this was certainly the case—only one MIII was found (in the sample from 1840 hr.). In the sample from 1600 hr., 65 per cent. of the males were MI and 35 per cent. MII, which would correspond with an emergence peak at 0900 hr. Direct inspections had been made at 0830 and 1130 hr., and it had been noted that there were already quite a few at the first inspection. Of course, these were very few compared with the enormous numbers at 1600 hr., but as at least 55 per cent. of those from 0830 hr. must have been MII at 1600 hr., they may have increased the relative number of MII slightly and thus have given an impression that the main emergence had been a little earlier than it actually was.

At 1840 hr. the percentage of MII had increased to 75, which would correspond very well with a peak of emergence at 1000 hr.

The migrants had the same proportion of MI and MII (26 and 74%, respectively, corresponding to an age of 8–9 hours). This showed that the vast majority of the mosquitos had left the area. Probably not more than one per cent. was left; but this was still enough to constitute a very large number. Of these we found that only 20 per cent. of the males were MII. This is the distribution of six-hour-old insects.

Three hours later, at 2200 hr., there were hardly any mosquitos left. Only after long and careful sweeping did we get a sample of 120 insects. Two-thirds of the males were MI and one-third MII.

From these observations we get a fairly clear picture of the age at which the migration starts. In a population with an average age of 8–9 hours the vast majority is ready to take off as soon as the conditions (probably a certain threshold of light) permit the migratory flight. Those left behind have an average age of six hours, and it, therefore, seems that when the insects are seven hours old they

are ready to migrate. During a second dispersal test (Provost, 1957), it had already been shown that individuals which became ready to leave after sunset will eventually start on their migration, and the present observations corroborate this.

In *Ascia*, we found that the female butterflies normally do not start on or continue a migration after maturation of the ovaries, which takes place at an age of about 30 hours. It is likely that there is an upper age limit for migration in mosquitos also, but it is not yet known.

The ratio of females to males in the samples mentioned above is rather difficult to understand. At 1600 and 1840 hr., females constituted 8 and 6 per cent., respectively, of the total, but 19 per cent. of the migrants were females and, of those left in the area after the departure, 29 per cent. were females, a figure which at 2200 hr. had increased to 43 per cent. How this should be interpreted is not clear and we will probably not be able to find an explanation until we have a better way of determining the age of females and until we know more about the hiding places of the females during the day.

Conclusions.

Although these observations give some insight into the conditions necessary for migration in mosquitos, they also pose a host of unsolved questions. Both locusts and butterflies perform extensive flights, circling and milling around (and in *Ascia*, feeding) between the departure from the resting places and the actual start of the migration. It is not known if this is so with mosquitos, but it is likely, and it should be emphasised that the only departure dealt with here is the take-off from the resting place. It is true that we know that the departure takes place only during the dark part of the 24 hours. We have also learned that the departure is delayed until some time after emergence, but here already we meet difficulties. In Fort Pierce the pre-migratory period seemed to be 7–13 and in Tampa 6–9 hours. It is difficult to explain why some individuals in the dusting experiments remained at the breeding places for 24 hours. Even if they had emerged shortly before sunset they would have been 10–11 hours old before dawn, yet they had not departed. It is possible that only those individuals which come to the age of migration before a certain hour (*e.g.*, midnight) will take off that night. This would be in agreement with the observation that individuals of *Ascia* usually do not start migrating after 1400 hr. One consideration should never be overlooked: we have seen the migrations start off from the breeding places in the evening and must suppose—somewhat by analogy from the butterflies—that they end up at another breeding place. This, indeed, proves to be the case when, a few days later, the males start swarming and the females biting. Even if they were migrating every night they would at least rest in the daytime, and we would expect to find in the breeding area an increasing number of emigrated MIII males from the day after emergence until swarming begins. Actually we never see the males again after their departure on migration except for the few minutes when they are swarming.

The male swarms are always found close to a potential breeding area. We have tried in the Fort Pierce area to make simultaneous observations at different distances from the breeding places, but no swarms were ever found more than 50–100 m. from a place known to us as a breeding area. We have learned a little about the conditions for the departure on a flight during which, as shown by Provost (1952, 1957), they are scattered far away. As to the flight itself we are completely ignorant.

Summary.

The departure of the newly emerged adults of the salt-marsh mosquito, *Aëdes taeniorhynchus* (Wied.) from the breeding sites was studied in Florida. The

departures, which are presumed to be the initial stage of the migratory flight, have been observed to take place only in the dark period of the 24 hours, and, the vast majority of individuals being ready to take off at dusk, spontaneous mass departure took place at that time.

Samples of the resting population of mosquitos were taken at intervals before and after the mass departure, and from the departing migrants. The average age of the males in each sample was estimated by the proportion in different stages of hypopygial rotation, from which it is concluded that migratory activity begins when the insects are six or more hours old. The end of the migratory period is not yet known. In all of 21 female departing migrants examined, the ovaries were immature and the spermathecae empty.

Acknowledgements.

The observations in Fort Pierce were carried out in collaboration with my wife, Mrs. Astrid Tetens Nielsen, who also performed the histological examinations; she was fatally ill during the observations in Tampa.

I am grateful to Mr. H. B. Crowell, Mr. James F. Sheldon and Mr. Jack Terrana of the Hillsborough County Health Department for their kind assistance during the work in Tampa.

The laboratory part of this work was carried out at Archbold Biological Station, Lake Placid, Florida. I am greatly indebted to Mr. Richard Archbold, President of the Archbold Expeditions, for his ever-ready assistance.

My best thanks are due to Dr. M. W. Provost for friendly discussions and linguistic correction of this manuscript.

Miss Hedvig Tetens Nielsen and Miss Kirsten Tetens Nielsen have in various ways assisted in the work.

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FIG. 1. Male with 90° rotation (Stage MII).

FIG. 2. Stage MI.

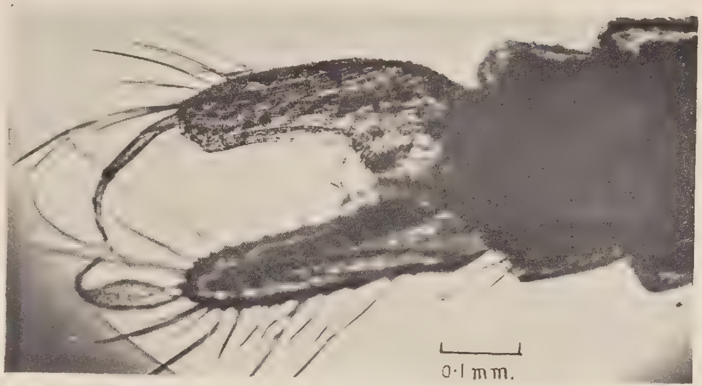

FIG. 3. Stage MII.

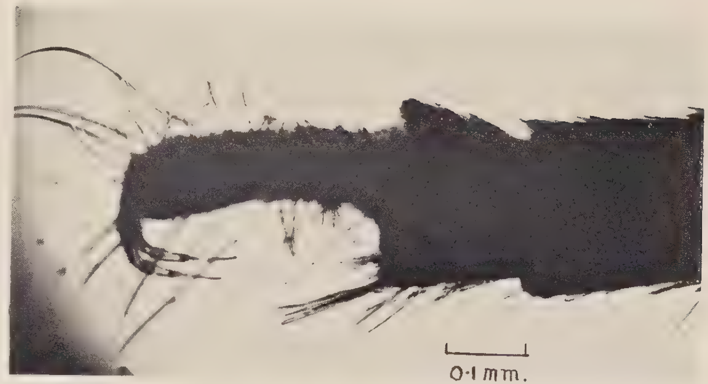

FIG. 4. Stage MIII.

STAGES IN HYPOPYGIAL ROTATION OF *AËDES TAENIORHYNCHUS.*

(In figures 2—4 the tip of the abdomen is seen from the right side of the insect.)

Spermathecae of *Aëdes taeniorhynchus:* one with spermatozoa, the other two empty. The full one appears larger because the section was closer to its centre than to the centre of the other two.

STUDIES ON AQUEOUS SUSPENSIONS OF INSECTICIDES.

PART VI. FURTHER NOTES ON THE SORPTION OF INSECTICIDES BY SOILS.

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Contents.

The striking behaviour of particles of insecticide sprayed on to some tropical soils was described in two previous papers (Hadaway & Barlow, 1952; Barlow & Hadaway, 1955). The particles of insecticide disappeared from the surface of blocks made of the soils kept at normal ambient temperatures and humidities in times ranging from a few hours for γ BHC to a few days for DDT. It was shown, with DDT, that all the insecticide could be recovered from the outermost layers of mud immediately after the particles had disappeared visually and that subsequently this sorbed DDT continued to diffuse slowly further into the block. After 12 months, the concentration was more or less uniform through the block, but no DDT had been lost. Dieldrin and γ BHC are being used extensively in tropical houses built with mud walls, and this paper contains the results of quantitative measurements on sorption of these insecticides. Previously, only biological measurements had been made. In addition, the residual effect on mud is measured at a range of dosages whereas only low dosages of dieldrin and γ BHC were used before. Gamma BHC is of especial interest because it is relatively volatile and the opposing actions of evaporation and adsorption were expected to be competitive. Finally some miscellaneous observations on the sorption of insecticides are included.

Materials and Methods.

Suspensions of pure dieldrin (recrystallised HEOD, m.p. 176°C.) were made in the size range 0–10 microns by the method previously described (Hadaway & Barlow, 1951). The γ BHC suspensions used were made from a Gammexane wettable powder containing 50 per cent. lindane. These suspensions were sprayed in a tower on to the test surfaces which were generally blocks made from a Uganda red soil. Other surfaces are described where they were used. The Uganda soil was the one which has been used as a " standard " in this series of papers. It

was sieved through a 30 I.M.M. sieve and made into large round blocks (7·4 cm. diameter by 1·2 cm. thick) for biological tests or small blocks (4·3 cm. diameter by 1·2 cm. thick) for chemical extractions and recoveries. These blocks were air dried for several weeks before use. After spraying, the blocks were kept in a large room at 25°C. and with a relative humidity of 50 to 70 per cent., the usual figure being about 60 per cent.

Biological tests were carried out at intervals by exposing blood-fed female mosquitos (*Aëdes aegypti* (L.)) to the sprayed surface of blocks by the method described previously (Hadaway & Barlow, 1951). No attempt was made to distinguish between fumigant and contact actions, and exposures were made under funnels on the large blocks. The relative humidity during the tests was always about 50 to 55 per cent. The numbers of dead were counted 24 hours after the exposures.

Also, at intervals, small blocks were sectioned by scraping away successive layers of mud starting with the sprayed surface. Each layer consisted of a weighed amount of mud, 0·25 g. for the first layer, 4·0 g. for five subsequent layers, and about 8·0 g. for the last which consisted of the remainder of the block. Each small block was therefore divided into seven layers. A weight of 0·25 g. represents a thickness of about 0·1 mm., and that of 4·0 g. a thickness of 1·7 mm. Each layer was extracted with 40–60 petroleum ether in a soxhlet for two hours. This solvent has been found in preliminary experiments with soil extracts to give low and reproducible blanks which were not appreciably higher than the reagent blanks. It could also be evaporated readily and thus minimised any losses of insecticides, especially γ BHC, due to evaporation. The extracts were evaporated to 5–10 cc. by boiling and the remaining solvent finally removed by immersing the flasks in luke-warm water and passing a stream of air over the surface of the evaporating solvent. The residues in the flasks containing γ BHC were dissolved in 1 cc. of acetone, and after 5 cc. of 2 per cent. potassium hydroxide in ethanol had been added the flasks were stood for at least an hour at room temperature. After acidification with 2 cc. of 2N acetic acid the contents of the flasks were titrated potentiometrically with N/200 silver nitrate solution (1 cc. = 0·48 mg. γ BHC). The coefficient of variation with replicates of 1·30 mg. of γ BHC was 0·6 per cent. The residues in the flasks containing dieldrin were dissolved in 5 cc. Analar isopropanol and 300 mg. of clean sodium added in small pieces. The flasks were attached to reflux condensers and the reaction promoted with a very small flame. After the sodium had completely reacted, 5 cc. of a 1:1 mixture of isopropanol and distilled water were added and, after cooling, the mixture acidified to phenolphthalein with 2N acetic acid. One cc. of acid was added in excess and the solution titrated with N/200 silver nitrate potentiometrically (1 cc. = 0·31 mg. dieldrin). The coefficient of variation with replicates of 2·00 mg. of dieldrin was 0·7 per cent.

Because γ BHC is volatile and losses have been found even during the evaporation of ether solutions (Hancock & Laws, 1955), a check was made as to whether any loss was appreciable with quantities such as were likely to be encountered in the present tests. Two mg. of γ BHC was added to each of a series of flasks containing 130 cc. of 40–60 petroleum ether, the volume normally used in the extraction process. The solvent was removed as described above and the amount of γ BHC in the residue compared with that found without addition and evaporation of solvent. The average recoveries were 1·95 mg. and 1·99 mg., respectively, indicating a possible loss of not more than 2 per cent. A similar experiment was also performed with 0·20-mg. quantities of γ BHC and the losses were not more than 5 per cent. even with this smaller amount.

DDT, used in a few tests, was determined by a modification of the Schechter-Haller method.

The amounts of the insecticides recovered from the mud blocks showed a

scatter around the nominal dosage due to the accumulated errors of sampling and chemical determination. This scatter, however, did not cover a range of more than about ± 10 per cent., and the results showed quite clearly whether or not a reduction in amount of insecticide in the mud was occurring.

The Sorption of γ BHC on Uganda Mud.

Blocks were sprayed with a γ BHC wettable powder at different dosages. The results of tests with mosquitos are given in Table I. The results at 25 mg. per sq. ft. were similar to those recorded previously (Hadaway & Barlow, 1952) while the higher dosages gave kills which were roughly proportional to dosage.

TABLE I.

Residual toxicity to *A. aegypti* of γ BHC on mud blocks.

Dosage (mg./sq. ft.)	Age of deposit	Percentage kill after exposure of . . . min.						
		0·25	4	8	16	32	64	128
100	1 hour	100						
	2 weeks		0	13	73			
	4 weeks			0	3	60		
	9 weeks				0	25	98	
	16 weeks					5	70	100
50	1 hour	100						
	2 weeks			0	8	60		
	4 weeks				0	8	65	
	9 weeks					0	50	100
	16 weeks					0	15	75
25	1 hour	100						
	2 weeks				0	5	70	
	4 weeks					0	3	63
	9 weeks						0	48
	16 weeks						0	8

Chemical determinations of the distribution of γ BHC in blocks sprayed with 100 mg. per sq. ft. are given in Table II. At the same time the rate of loss of γ BHC deposits from glass plates was also measured (Table III) so as to provide

TABLE II.

The average percentage distribution of γ BHC in successive layers of Uganda mud blocks.

Layer no.	Wt. of layer (g.)	Time after spraying (weeks)						
		0	1	2	4	8	16	32
1	0·25	92	3	1	1	0	1	16
2	4·0	8	49	33	21	15	14	
3	4·0	0	30	27	19	16	14	11
4	4·0		14	19	16	15	14	15
5	4·0		4	10	14	14	15	14
6	4·0		0	5	12	13	13	11
7	8·0		0	5	17	27	28	33
Av. wt. of insecticide recovered (mg./sq. ft.)		105	100	108	105	86	48	24

some indication of the increase in residual action which sorption gives to a relatively volatile insecticide.

It is evident that γ BHC diffused further into the blocks after the initial sorption much more rapidly than DDT (Barlow & Hadaway, 1955). The concentration of insecticide was almost uniform throughout the blocks within eight weeks after spraying. There were no appreciable losses of γ BHC until the condition of uniform concentration was being approached. On the other hand loss of insecticide from glass plates was rapid and progressive. There was a loss of 50 per cent. in the first week after spraying and none remained after four weeks.

TABLE III.

Evaporation of γ BHC from glass plates.

Time (weeks)	0	1	2	4
Av. wt. recovered (mg./sq. ft.) ..	106	50	6	0

The Sorption of Dieldrin on Uganda Mud.

Previous tests with dieldrin showed that, at a dosage of 25 mg. per sq. ft., the contact action fell rapidly as sorption occurred and, after a week, kills were very low even after an exposure of 128 minutes. It was stated (Hadaway & Barlow, 1952) that the contact action of dieldrin was lost after sorption but it would have been better to have said that it was very greatly reduced, as the following experiments show that it is possible to obtain high kills with very long exposures such as might occur in treated houses or if the dosage of dieldrin is raised.

Mud blocks were sprayed with a dieldrin wettable powder or with a suspension of 0–10 micron crystals of dieldrin. The results of tests with mosquitos are given in Table IV. Again, as with γ BHC, the kills at any one time were roughly

TABLE IV.

Residual toxicity to *A. aegypti* of dieldrin-treated mud blocks.

Formulation of dieldrin	Dosage (mg./sq. ft.)	Age of deposit	Percentage kill after exposure of . . . minutes						
			0·25	8	16	32	64	128	256
Pure, 0–10μ suspension	100	2 hours	100						
		19 days		0	15	58	100		
		53 days				0	25	85	
		16 weeks				0	13	65	
		24 weeks					0	3	18
50 per cent. wettable powder	100	2 hours	100						
		19 days			3	15	53		
		53 days				0	10	35	
	50	2 hours	100						
		19 days				0	3	88	
		53 days					0	15	83
	25	2 hours	100						
		19 days					0	10	28
		53 days							0

proportional to the dosage of dieldrin used and probably, therefore, to the concentration near the surface of the blocks.

Chemical determinations of the distribution of the dieldrin in blocks treated with 100 mg. per sq. ft. of the 0–10 micron suspension are shown in Table V. Glass plates were sprayed with the same suspension at the same time, and the rate of loss of dieldrin is shown in Table VI. Dieldrin did not reach a uniform concentration throughout the blocks in 24 weeks and there was substantially no loss of insecticide from the blocks in 48 weeks, whereas about 50 per cent. was lost by evaporation from glass plates in 24 weeks, and 90 per cent. was lost in 52 weeks. Dieldrin appears, therefore, to be intermediate in behaviour between γ BHC and DDT in volatility. This is in agreement with differences in the rate of sorption of the three insecticides.

TABLE V.

Average percentage recoveries of dieldrin from successive layers of Uganda mud blocks.

Layer no.	Wt. of layer (g.)	Time after spraying							
		2 hours	1 day	6 days	21 days	56 days	16 weeks	24 weeks	48 weeks
1	0·25	86	25	13	4	3	3	2	1
2	4·0	14	74	79	49	35	27	23	17
3	4·0	0	1	8	30	27	22	20	16
4	4·0	—	0	0	16	18	17	16	15
5	4·0	—	—	—	1	10	13	13	14
6	4·0	—	—	—	0	4	9	10	14
7	8·0	—	—	—	—	3	10	17	24
Av. weight recovered (mg./sq. ft.)		110	94	110	107	100	112	91	101

TABLE VI.

The loss of dieldrin from glass plates.

Time	0	11 weeks	24 weeks	52 weeks
Av. deposit (mg./sq. ft.) ..	100	84	50	10

Identification of Insecticides Recovered from Mud Blocks.

The analytical methods used to determine γ BHC and dieldrin are not specific, and although in previous work DDT had been recovered and identified as such after 12 months in the adsorbed state it was thought that it would be more satisfactory if it could be confirmed that γ BHC and dieldrin did not undergo any chemical change on adsorption on this soil. A further check was also made on the recovery of p,p′DDT.

Blocks were sprayed with suspensions of γ BHC, dieldrin and DDT, and after 14 days the blocks were ground and extracted with 40–60 petroleum ether for 8 hours. The extracts were concentrated, made up to 25 cc., and aliquots analysed in the usual way for the insecticides. The weight of each expected was calculated from the area of four large blocks sprayed at 100 mg. per sq. ft.

(*a*) *Qualitative colour tests.*

(*i*) *Dieldrin.*—A sample of the extract containing 0·45 mg. was evaporated to dryness and the residue dissolved in 0·1 cc. xylene. After 2 cc. of fuming sulphuric acid had been added a red colour developed immediately and intensified on shaking. The same depth of colour was given when 0·45 mg. of recrystallised dieldrin was tested in the same way. This test is described by Johnson (1956).

TABLE VII.

Recovery of sorbed insecticides from Uganda mud blocks.

Insecticide	mg. expected	mg. found	% recovery
Dieldrin ..	19·2	18·3	95
DDT	19·2	18·6	97
γ BHC ..	19·2	18·3	95

(*ii*) *DDT.*—This was sufficiently characterised by the blue colours developed in the analytical method, a modification of the Schechter-Haller method.

(*iii*) γ *BHC.*—Similar colour tests, which are specific, are not available for γ BHC.

(*b*) *Paper chromatography of the extracts.*

Further information on the identity of the insecticides was obtained by paper chromatography, using the methods described by Barlow (unpublished). Sufficient of each extract to contain about 4 to 5 μg. of insecticide was spotted on to paper impregnated with liquid paraffin. The moving solvent was 80 per cent. ethanol. Corresponding amounts of pure materials were run on adjacent portions of the paper. Each extract contained only one chlorinated component and the Rf values were the same as those of the pure materials.

This solvent system will separate decomposition products of dieldrin and DDT and so the chromatography provided more evidence for lack of decomposition of the sorbed insecticides. It is also fairly conclusive for γ BHC although trichlorobenzenes, the usual decomposition products, are too volatile to be chromatographed on paper. However, the combination of the observations that the substance in the extract had the same Rf as γ BHC and had about the correct content of labile chlorine, as shown in Table VII, leaves little doubt as to its identity.

Dieldrin extracted from a Uganda mud block 12 months after spraying was also detected on a chromatogram and again only the insecticide itself was present.

(*c*) *Crystallisation of the recovered insecticides.*

Finally the insecticides remaining in the extracts were recrystallised and their melting points determined.

Crystallisation was not easy because of the large amounts of oily and waxy material extracted from the soil along with the insecticides. Chromatography on alumina failed to purify the extracts. Sublimation was only partially successful with γ BHC and, at the temperature required for DDT and dieldrin, an oily impurity distilled as well. At last it was found that the impurities were relatively insoluble in methanol. Therefore the residues of each extract, after removal of the solvent, were extracted with small portions, 0·1 to 0·2 cc., of hot methanol and the extracts transferred to small test-tubes. The solvent was evaporated and each insecticide crystallised from a small volume of methanol. A few traces of

the oily impurities still remained so the insecticides were recrystallised. Naturally all these manipulations greatly reduced the yields but enough of each insecticide was obtained to determine the melting points and mixed melting points which are given in Table VIII.

TABLE VIII.

The properties of insecticides recovered from Uganda mud blocks.

Insecticide	Weight in extract (mg.)	Wt. of crystalline material recovered (mg.)	Melting point (°C.)	Mixed melting point (°C.)
Dieldrin ..	18·3	5·6	175–176	175
DDT	18·6	7·4	107–108	107–108
γ BHC ..	18·3	10·2	112	112·5

The possible Decomposition of Dieldrin by Acidic Soils.

Both the tests described on pages 319–321 and the biological activity of the mud blocks (Tables I & IV), which only decreases as the actual concentrations of insecticides at the surface decrease, may be taken as conclusive evidence that decomposition is of no importance in the behaviour of the insecticide on the standard Uganda soil used.

There remains the possibility of decomposition on other soils, although this is unlikely because the sorption phenomenon is a general one and varies only in degree from one soil to another. The decomposition of DDT catalysed by iron compounds only occurs under anhydrous conditions which would not be met in practice (Hadaway & Barlow, 1952). DDT and γ BHC might also suffer dehydro-halogenation on basic soils, but DDT has been identified, by the colorimetric analytical method used, after sorption on a sufficiently wide range of soils to render such a possibility unlikely. Dieldrin and related compounds, on the other hand, are more likely to decompose when sorbed on soils of high " surface acidity " (Shell Chemical Corporation, 1954, p. 77). Sorbed dieldrin has only been recovered and identified from the standard Uganda soil, whose pk_a is between $+3$ and $+4{\cdot}5$. That is to say, the surface acidity is not high enough to be a potential cause of decomposition. The surface acidities of all the soil samples available to us were therefore determined with solutions of Hammett's indicators. The method used by Shell " Research " Limited, was described to us by Dr. J. K. Eaton. Determinations could frequently only be made very roughly because of the dark colour of the samples. However, only two, one from Entebbe, Uganda, and one from Lagos, Nigeria, appeared to have a pk_a of between $-2{\cdot}2$ and $+1{\cdot}5$ and might, therefore, cause decomposition. Blocks of these soils were sprayed with 100 mg. per sq. ft. of a 0–10 micron suspension of dieldrin and, after sorption was complete, the blocks were extracted in the usual way. Samples of each extract were tested by paper chromatography and there was no indication of decomposition of the dieldrin. The system used was capable of giving a clear separation of the products of dieldrin decomposition under acidic conditions (Barlow, unpublished). Therefore, it seems that sorption of dieldrin proceeds without decomposition even on soils of high surface acidity.

The Sorption of Insecticides from the Vapour Phase by Mud Blocks.

It was shown in Part III of this series (Hadaway & Barlow, 1952) that γ BHC vapour could be sorbed by Uganda mud and it was concluded in Part V (Barlow & Hadaway, 1955) that the normal sorption could proceed via the vapour phase

as it was possible to show by calculation that evaporation of the crystals at a maximum rate could account for the observed rates of disappearance. However, no quantitative measurements of the uptake of vapour had been made. These have now been done and indicate that the vapour phase is of only very minor importance in the transfer of insecticide from particles to the active surface of the mud. By far the greatest movement must be brought about by diffusion directly from the crystals over the surface of the soils.

Small filter papers, 5·5 cm. in diameter, were treated with γ BHC, dieldrin or DDT by applying a solution of the insecticide in 40–60 petroleum ether from a pipette. The dosages applied were approximately 100 mg. per sq. ft. The dosages used were checked by extracting some of the papers immediately after impregnation and measuring the insecticide contents of the extracts. Each of the papers to be used in the tests was placed between two small brass rings of the type used as moulds for small mud blocks so that it was held firmly in a horizontal position. A small mud block (4·3 cm. diameter by 1·2 cm. deep) covered with an untreated 4·25 cm. filter paper was placed inside the lower ring. The distance between the nearest surface of the block of dried mud and the treated filter paper was about 0·5 to 1·0 mm. The smaller paper was laid directly on the mud itself to ensure that no particles of insecticide could fall on to the mud from the treated paper. Each assembly was placed in a desiccator at 10 per cent. R.H. This humidity was chosen because, as shown in the next paper of this series (Barlow & Hadaway, 1958), low humidities favour rapid sorption of insecticides. At intervals after the experiment began, the following samples were taken from each assembly and their insecticide content measured:

1. The impregnated paper.
2. The untreated paper lying on the mud block.
3. Successive layers of mud from the block.

Thus it was possible to determine how much of the insecticide lost from the paper had been taken up by the mud block lying beneath but not touching it. Recoveries, in mg. of γ BHC, are shown in Table IX. It can be seen that the insecticide evaporates rapidly from the paper lying close to the mud surface but only about half of it is sorbed by the mud. That is to say the mud only takes up that part of the evaporating vapour which diffuses from its own side of the paper. Similar results were obtained with dieldrin and DDT although naturally the rates of evaporation were very much slower. Table X gives the figures in mg. of insecticide recovered for these insecticides but in a shortened version corresponding to Table IX, the mud fractions being added together.

TABLE IX.

The sorption of γ BHC vapour by mud blocks.

Sample	Time (days)			
	0	7	14	21
Impregnated paper	2·46	0·12	0·00	0·00
Untreated paper covering mud block	—	0·00	0·00	0·00
First layer of mud, 0·25 g.	—	0·34	0·24	0·21
Second " " " 4·0 g.	—	0·79	0·96	1·01
Third " " " 4·0 g.	—	0·01	0·00	0·02
Fourth " " " 4·0 g.	—	0·00	0·00	0·00
Total recovery (mg.) : wt. of insecticide from paper plus weight of insecticide from the mud	2·46	1·26	1·20	1·24
Recovery (mg.), wt. of insecticide from paper plus twice the weight of insecticide from the mud	2·46	2·40	2·40	2·48

Therefore, if the insecticide particles are moved any appreciable distance from the surface of the mud blocks, the rate at which their vapour molecules can be taken up does not provide anything approaching a possible reason for the dramatic rate of disappearance of the particles and their quantitative recovery on the mud. Also, there is no obvious reason why reducing the gap between insecticide and mud should change the picture in any fundamental way until actual contact between the two is made.

TABLE X.

The sorption of dieldrin and DDT vapours by mud blocks.

Insecticide	Sample	Time (days)			
		0	7	21	51
Dieldrin	Impregnated paper..	2·29	2·12	1·09	0·51
	Total mud recovery	—	0·11	0·55	0·87
	Total recovery (mg.) paper and mud	2·29	2·23	1·64	1·38
	Total recovery (mg.) paper and twice wt. on mud	2·29	2·34	2·19	2·25
DDT	Impregnated paper	2·35	2·20	2·10	2·04
	Total mud recovery	—	0·04	0·12	0·20
	Total recovery (mg.) paper and mud	2·35	2·24	2·22	2·24
	Total recovery (mg.) paper and twice wt. on mud	2·35	2·28	2·34	2·44

However, there is still something about the process which is not understood because in further experiments of this type with γ BHC a very clear influence of the mud on the natural evaporation rate of the insecticide from the paper was noticed. These experiments were conducted as before except that mud blocks were not placed beneath some of the impregnated papers, and that a cabinet at 30 per cent. R.H. was used instead of desiccators to lessen the possibility of interaction between adjacent samples which might happen with vapours in a confined space. Recoveries of γ BHC from the papers are given in Table XI and it is clear that although the mud only takes up that amount of insecticide which vapourises from its own side of the filter paper it greatly accelerates the general rate of evaporation.

TABLE XI.

The influence of active mud blocks upon the rate of evaporation of γ BHC from filter papers.

	Time after preparation (days)			
	0	3	7	21
Wt. of insecticide (mg.) on papers over mud blocks	2·46	0·64	0·20	0·00*
Wt. of insecticide (mg.) on papers not over mud blocks	2·46	1·56	0·95	0·02

* The mud blocks under these papers were sampled and contained an average of 1·18 mg. γ BHC.

Measurements on the Sorption of DDT and Dieldrin on other Soils.

In all the previous work on quantitative recovery of adsorbed insecticides only the standard Uganda red soil, which is a very active adsorbent, has been used.

A few experiments were therefore made with two less active soils. A grey one from Delhi and a red one from Taveta, Kenya, were compared with the standard Uganda soil.

The blocks were sprayed with DDT or dieldrin as 0–10 micron suspensions at 100 mg. per sq. ft. and were stored in desiccators at 25°C. and 50 per cent. R.H. They were sectioned at intervals but unfortunately the sampling of Taveta blocks could not be done in exactly the same way as the other two because the soil was of such a loose, gritty texture that the usual 0·25-g. outer layer could not be removed satisfactorily. In order to sample an even layer it was necessary to make this outer layer twice as deep.

Visually, both dieldrin and DDT disappeared much more slowly from the Delhi and Taveta soils than from the Uganda soil. This is borne out by the recoveries, shown in Table XII, of dieldrin and DDT from the smallest outer layer at 4 and 6 days, respectively. Some penetration had occurred, however, and both dieldrin and DDT continued to diffuse inwards especially on the Delhi soil. However, the diffusion was much slower than in the Uganda soil. There were no visible signs of surface deposits of either insecticide on the two less-active soils on the last days of sampling, 13 and 28 days for dieldrin and DDT, respectively.

TABLE XII.

Average percentage distribution of dieldrin and DDT in three tropical soils.

Soil	Layer no.	Dieldrin				DDT			
		Wt. of layer (g.)	Time (days)			Wt. of layer (g.)	Time (days)		
			0	4	13		0	6	28
Uganda, red ..	1	0·25	92	17	10	0·25	93	15	10
	2	4·0	8	79	67	2·0	6	63	39
	3	4·0	0	5	20	2·0	1	18	21
	4	4·0	—	—	4	2·0	—	4	14
	5	4·0	—	—	0	2·0	—	—	9
	6	4·0	—	—	—	2·0	—	—	5
	7	8·0	—	—	—	2·0	—	—	3
Delhi, grey ..	1	0·25	94	56	30	0·25	92	70	30
	2	4·0	6	44	68	2·0	8	30	59
	3	4·0	0	0	2	2·0	0	0	10
	4	4·0	—	—	0	2·0	—	—	1
	5	4·0	—	—	—	2·0	—	—	0
Taveta, red ..	1	0·50	93	73	65	0·50	90	83	68
	2	4·0	6	27	35	2·0	10	17	31
	3	4·0	1	0	0	2·0	0	0	1
	4	4·0	—	—	0	2·0	—	—	0
	5	4·0	—	—	—	2·0	—	—	0

The Effect of removing some Constituents of the Uganda Soil.

Two modifications have been made to the standard Uganda soil to see if the adsorptive properties were thereby affected. (a) Small samples were extracted with benzene for eight hours, dried and made into blocks after regrinding to pass a No. 30 I.M.M. sieve. Removal of all materials soluble in organic solvents did not change the properties of the soil (Table XIII). (b) The soil was boiled with successive portions of dilute (6N) hydrochloric acid until it was free from iron compounds. After washing free from the acid it was dried and ground. The product was a light-grey powder consisting of 74 per cent. of the original soil.

It was made into small blocks which were tested in the usual way by carbon tetrachloride sorption and by visually observing the disappearance of 0–10 micron particles of DDT and dieldrin from the surface. This Uganda soil with iron removed was still highly active against dieldrin although DDT was not lost from the surface so readily (Table XIII). However, removal of iron had certainly not made it inactive.

TABLE XIII.

The properties of modified Uganda red soil.

Sample	CCl_4 sorption	Approx. time for loss of DDT at 100 mg./sq. ft.	Approx. time for loss of dieldrin at 100 mg./sq. ft.
Uganda soil	21·4	2–3 days	< 24 hours
Uganda soil extracted with benzene	25·6	2–3 days	< 24 hours
Uganda soil without iron	32·9	10–14 days	< 24 hours

Temperature and the Diffusion of DDT and Dieldrin in Mud Blocks.

It has been observed in Part V of this series of papers (Barlow & Hadaway, 1955) that an increase in temperature gave an increased rate of sorption as judged visually by watching the particles disappear from the mud surface. These observations have been repeated. Small mud blocks were sprayed with 100 mg. per sq. ft. of 0–10 micron crystals of DDT and immediately placed in desiccators at 50 per cent. R.H. and one of the temperatures, 20, 25 and 30°C.

After 24 hours there was an obvious gradation, the rate of disappearance increasing with temperature.

Temperature might also be expected to influence the rate of diffusion of insecticides within the blocks after sorption was complete. Small blocks sprayed at the same time as the ones above were stored at 50 per cent. R.H. and 25°C. for four weeks and the distribution of the DDT then determined in samples. The remaining blocks were then kept at 50 per cent. R.H. but were divided between three temperatures, 20, 25 and 30°C. Blocks from each desiccator were sampled at four and eight weeks after placing at the new temperature. It can be seen from the results given in Table XIV that temperature appeared to have a small effect upon the rate of diffusion of DDT but it was not very striking.

TABLE XIV.

The influence of temperature (°C.) upon the diffusion of DDT sorbed in mud blocks.

Layer no.	Wt. of layer (g.)	Time after transfer to different temperatures (weeks)						
		0	4			8		
			20°	25°	30°	20°	25°	30°
1	0·25	10	6	5	5	4	5	3
2	4·0	60	48	44	38	45	38	36
3	4·0	22	22	24	25	23	24	23
4	4·0	8	13	14	15	13	15	16
5	4·0	—	6	7	9	9	9	10
6	4·0	—	2	3	5	3	5	6
7	8·0	—	3	3	5	3	4	7

A similar experiment was performed with dieldrin. Small blocks of Uganda mud were sprayed with 100 mg. per sq. ft. of 0–10 micron crystals of dieldrin and immediately placed in desiccators at 25°C. and what was thought to be 50 per cent. R.H. After three weeks the distribution of the dieldrin in the blocks was determined and found to be of a type which suggested that the humidity in the desiccators was much lower than intended. It was indeed found that the specific gravity of the sulphuric acid solutions corresponded to a R.H. of about 25 per cent. and a mistake had been made in the preparation of the solutions. This was annoying but also encouraging in that it supported the validity of the relationship found experimentally between R.H. and sorption which is given in Part VII of this series (Barlow & Hadaway, 1958).

The distribution in the blocks was known, however, and these were divided into two groups. Both were kept at 50 per cent. R.H. but one was kept at 30°C. and the other at 18 to 20°C. Samples of each group were taken three and six weeks later, and the results are given in Table XV. Again the diffusion appeared to be more rapid at the higher temperature.

TABLE XV.

The influence of temperature upon the diffusion of dieldrin sorbed in mud blocks.

Layer no.	Wt. of layer (g.)	Time after transfer to different temperatures (weeks)				
		0	3		6	
			18–20°C.	30°C.	18–20°C.	30°C.
1	0·25	20	10	5	11	4
2	4·0	80	78	64	67	52
3	4·0	0	12	24	18	28
4	4·0	0	0	8	4	13
5	4·0	—	0	0	0	4
6	4·0	—	—	—	0	0
7	8·0	—	—	—	0	0

Repeated Applications of DDT and Dieldrin.

It is of interest to know whether the rate of sorption of an insecticide on one of these active muds is influenced by previous applications. Any influence would be unexpected because it is only the surface layers of mud which are concerned with the primary adsorption from the solid phase, and the concentration of insecticide in these from a previous spraying becomes very low even in a week or two. It is unlikely that successive applications in the field would be made at intervals of less than several months.

Blocks were sprayed with 0–10 micron suspensions of DDT or dieldrin at 100 mg. per sq. ft. five times with a month between each spraying. The superficial, visible deposits of insecticide disappeared at about the same rate at each time of spraying, even though the amount of insecticide, especially dieldrin, on the blocks was much greater before the fifth spraying than would be likely to be encountered in practice.

Two weeks after the fifth spraying the blocks were divided into layers and the insecticide distributions determined as shown in Table XVI.

Of course, although the initial adsorption occurs at the normal rate, multiple applications give increased concentrations of insecticide at any one place in the mud. Thus, two weeks after a single spraying with dieldrin at 100 mg. per sq. ft. the concentration of insecticide in the thin outer layer of mud, 0·1 mm. in

depth, was equivalent to about 9 mg. per sq. ft. whereas two weeks after the fifth spraying at monthly intervals it was about 28 mg. per sq. ft. Therefore, a better biological effect would always be expected after repeated applications simply because diffusion of insecticide into the insect is likely to depend upon the concentration of insecticide in the superficial layer of mud.

TABLE XVI.

The percentage distribution of dieldrin and DDT in mud blocks after repeated sprayings.

Layer no.	Wt. of layer (g.)	Dieldrin	DDT
1	0·25	6	7
2	4·0	48	56
3	4·0	22	18
4	4·0	11	8
5	4·0	6	5
6	4·0	3	2
7	8·0	5	4

Discussion.

The results presented in this paper provide more information about the sorption of insecticides by certain soils which are used for house-building and therefore frequently serve as substrates for deposits of insecticides.

Previously it was shown that aldrin, γ BHC, dieldrin and DDT all disappeared from the surface of blocks made from a lateritic Uganda soil within a very short time when used at a dosage of 25 mg. per sq. ft. (Hadaway & Barlow, 1952). This physical loss of insecticide, attributed to a sorption process, was accompanied by an almost complete reduction in contact toxicity of the dieldrin- and DDT-treated blocks. Gamma BHC and aldrin, although suffering a marked reduction in activity, still continued to kill mosquitos for a considerable time, and this more prolonged effectiveness was considered to be due to fumigant action. DDT was also used at much higher dosages of 100, 200, or 400 mg. per sq. ft. and still suffered a great reduction in activity after times which varied with the dosage used. DDT, however, is a less potent insecticide than γ BHC or dieldrin for mosquitos and it was therefore thought desirable to see how these two insecticides behaved at dosages higher than the 25 mg. per sq. ft. used before. At the same time, chemical determinations of the distribution of γ BHC and dieldrin in mud blocks at various times after sorption were made to see if these two compounds behaved in the same way as DDT.

Gamma BHC and dieldrin at 25, 50 and 100 mg. per sq. ft. on Uganda mud blocks all gave complete kills of mosquitos with an exposure of a quarter of a minute immediately after spraying. All deposits of both insecticides were rapidly sorbed and when this process was complete the biological activities of the blocks were greatly reduced and were now roughly proportional to the dosage used. This was a reasonable result because the concentration of insecticide in the surface layers of mud, upon which the mosquitos rest, must depend upon dosage sprayed, and presumably the diffusion of an insecticide from the mud into the insects will depend upon its concentration. At any one dosage level the biological activity of the blocks fell gradually with increasing time after spraying. The rate of change of activity also decreased with time and this perhaps may be related to the probability that the rate of reduction of insecticide concentration

in the surface layers of mud, brought about by diffusion further into the blocks, will be dependent on concentration and will therefore become less with time.

However, the biological activities of all the blocks did decrease progressively and, despite the unusually high dosages used, dieldrin was only giving low kills after exposure of mosquitos for four hours 24 weeks after spraying. Sixteen weeks after application at the highest dosage of 100 mg. per sq. ft., γ BHC gave about the same kill in one hour as dieldrin did in two and this better performance is almost certainly due to the more pronounced fumigant properties of γ BHC. The commercial wettable powder of dieldrin gave lower kills than an equivalent dosage of pure dieldrin. This might be due to the lower concentration of active component (HEOD) in the powder or to a difference in particle size distribution between the two suspensions. The initial particle size distribution is known to influence the subsequent activity of the blocks after sorption of the insecticide.

The chemical determinations of distribution of γ BHC and dieldrin in the blocks at different times agreed qualitatively with the results obtained before with DDT (Barlow & Hadaway, 1955, Table III, p. 550). That is, all three insecticides were concentrated in the surface layers of mud shortly after the initial sorption was completed and thereafter diffused further into the blocks. The rates of this diffusion were in the same order as the rates of sorption for γ BHC and dieldrin. Thus, whereas the concentration of γ BHC was more or less uniform throughout the blocks after eight weeks, dieldrin required about 12 months to reach this stage. Dieldrin was sorbed more rapidly than DDT but appeared to diffuse inwards at more or less the same rate. It might be expected that in this type of phenomenon molecular sizes and shapes will have some influence on the behaviour of the different insecticides.

It was anticipated that the total amount of γ BHC recovered from the blocks would decrease with time due to losses by desorption and evaporation. Decreases in recovery did occur but only became definite and progressive after four to eight weeks when the concentration of insecticide throughout the depth of the blocks was approaching uniformity. It is interesting, and may be significant, that this is about the time when the rate of change of biological activity becomes notably slower. Possibly the insecticide may be reaching the mosquitos by several mechanisms, each of which becomes predominant at different times after spraying, depending upon exposure times and concentration of γ BHC in the surface layers of mud. Thus, immediately after mud blocks are sprayed with suspensions, the insects pick up high concentrations of insecticide as particles. When sorption is complete, biological activity must depend upon diffusion of insecticide from the mud blocks, but concentration will be high in the surface layers of mud and consequently median lethal exposure times will be relatively short. These exposure times will, however, increase rapidly because of rapid diffusion of insecticide further into the blocks. Once desorption of γ BHC vapour begins, fumigant action will become more important but then biological activities will change more slowly as desorption is a slow process.

Dieldrin showed negligible desorption even after 12 months, thus behaving like DDT. Sorption extended the residual lives of γ BHC and dieldrin but, practically, this effect was especially important for γ BHC. For instance, 50 per cent. of 100 mg. per sq. ft. of γ BHC on glass was lost by evaporation in one week, and none remained after four weeks. If the same dosage was sorbed on mud, 50 per cent. loss required 16 weeks. As the sorbed insecticide can still exert some biological action, the residual life is effectively prolonged. This beneficial influence in the case of dieldrin is obscured by the low relative activity of sorbed dieldrin. Dieldrin at 100 mg. per sq. ft. lost 50 per cent. of its weight in six months and 90 per cent. in 12 months from glass, whereas, as mentioned above, no desorption from mud occurred in 12 months. Although there are no biological results for the residues on glass, the portion of insecticide which did remain on the glass

would certainly be more effective biologically than the much greater amount that is sorbed in the mud.

It has sometimes been asserted in the past that chemical decomposition is of importance in the loss of activity of DDT on soils. It has already been shown that this does not happen with DDT on the soils we have tested (Barlow & Hadaway, 1955, p. 550). In this paper, experiments are described which confirm that this is also true for γ BHC and dieldrin as well as DDT. All these insecticides have been recovered from mud blocks after sorption and conclusively identified.

In Part V of this series (Barlow & Hadaway, 1955, p. 548) it was suggested that sorption of insecticides occurs via the vapour phase and reasons were given for this supposition. No quantitative measurements were made, however, and the results now obtained and shown in Tables IX and X do not support this idea. If the insecticide deposits are moved a small distance away from the surface of the mud blocks the mud will only sorb about half of the insecticide which evaporates, that is, only the portion of vapour which happens to diffuse in its direction. Therefore, if sorption of the insecticide depended upon the normal rate of evaporation it would be very much slower than is actually observed and would not permit collection of all the insecticide which is lost from the particles. It therefore seems that actual contact between the insecticide particles and the mud is necessary and sorption is more likely to be due to a surface diffusion process, a layer of insecticide molecules moving from the crystal lattice over the active surface of the mud.

The portion of the insecticide which does evaporate naturally can, of course, be sorbed from the vapour phase and there does seem to be something peculiar about this because in the tests just mentioned evaporation of γ BHC from filter papers was definitely greater when the papers were over mud blocks than when they were not. Dieldrin also seemed to evaporate more rapidly from papers over the mud than would have been expected from its rate of evaporation from glass. Admittedly the physical condition of the insecticide impregnated on paper cannot have been the same as in the dried spray deposits on glass, but even allowing for this, there seems to have been an unusually high rate of evaporation from the papers. A possible reason is that vapour was sorbed on to the protective filter paper lying on the blocks in small amounts not detected by the analytical method used and was then transmitted by surface diffusion to the mud, but in this case the mud would be expected to take up more than half of the evaporated insecticide. This action of mud at a distance remains a mystery unless it is in some way an experimental artifact.

Practically all the detailed biological and chemical measurements have been made with a single sample of highly active soil from Uganda. It is known that sorption of the insecticides can occur on other soils at varying rates and it would be useful to know what quantitative changes in distribution are involved when sorption takes place on less-active soils. A lot of work beyond our resources would be needed to do this properly, but a few experiments have been made on two soils of low activity on which sorption of DDT, for instance, takes weeks instead of days. Chemical measurements on these soils showed that just as the initial sorption was slow so was subsequent diffusion. This is perhaps not surprising as the two are inter-related to the extent that rate of diffusion inwards at any one time depends upon concentration of insecticide in the surface layers of mud which in turn depends upon the amount of insecticide which has been sorbed.

Whether sorptive activity is a property of the whole or only part of a particular soil is not known and in any case the relationship will most probably vary from one soil to another. The effect of removing two constituents of the standard Uganda soil has been investigated. Mud which was extracted with an organic solvent until all the waxy material of vegetable origin had been removed

showed no change in properties. Removal of all the iron oxides from the soil resulted in some loss of activity to DDT but none to dieldrin. Iron oxides as such are therefore not essential for activity. The treatment necessary to remove the iron may, of course, have activated some other constituent of the soil as activity is certainly not restricted to one particular type of chemical structure.

Tests have also been made on climatic factors which influence the sorption of insecticides on soils. Those which deal with humidity are reported in Part VII of this series of papers (Barlow & Hadaway, 1958). Temperature has a marked influence on the initial sorption. This is a diffusion process involving movement of molecules from crystalline particles of insecticide to the mud, and so an increase in temperature produces an increase in speed of sorption with any of the insecticides. Subsequent diffusion further into the mud blocks is only slightly influenced, at least over the temperature range and time intervals used.

There was no reason to believe that successive applications of an insecticide to a given sample of active soil would behave differently, providing a time interval greater than that necessary for sorption was allowed between each application. However, a few experiments were carried out to test this possibility because suggestions that it might occur in practice in the field have been made. Mud blocks were sprayed five times at monthly intervals with DDT or dieldrin but the insecticides disappeared in about the same time on each occasion. The successive sprayings did, of course, give progressively higher concentrations of insecticides at any level in the blocks, and therefore better biological action would be expected after each spraying. Also there would be greater recoveries of insecticides from samples such as those obtained by scraping shallow layers of mud from sprayed walls. Langbridge (1956), in Nigeria, found about 2·5 times the amounts of DDT and dieldrin in the surface half-millimetre after a third application as after the first.

A build-up of γ BHC in mud blocks after repeated applications will depend, of course, upon the time intervals between successive sprayings. If the time between two sprayings is sufficiently long, then desorption of γ BHC will proceed and there may be a total loss of the insecticide before the second application is made.

Summary.

Quantitative measurements of the sorption of γ BHC and dieldrin in Uganda mud blocks have been made. Gamma BHC diffused more rapidly than dieldrin, and within a few weeks had achieved an almost uniform concentration throughout the sprayed blocks. Only when the uniform concentration had been reached did loss by evaporation from the blocks become marked. Increased dosages of γ BHC gave increases in biological activity which were roughly proportional to the dosages used. Sorption on to mud greatly prolonged the residual life of γ BHC as compared with similar deposits on glass.

Dieldrin behaved in the same way as γ BHC although because of its slower rate of diffusion the distribution in the blocks had only reached in 48 weeks the stage reached by γ BHC in eight weeks. There was no appreciable loss of dieldrin during this time, whereas about 90 per cent. of the deposit on glass plates had been lost.

Gamma BHC, dieldrin and DDT were recovered from the adsorbed state on mud and identified. Any decomposition is therefore likely to be negligible. Dieldrin was also recovered from two soils which had much higher "surface acidities" than the standard.

Active mud can only sorb the portion of insecticide vapour from an evaporating deposit which happens to diffuse in its direction. This is to be expected, but the system has some peculiarities because the evaporation of γ BHC from filter papers over mud blocks is much faster than in the absence of the mud.

Measurements of the distribution of DDT and dieldrin in soils less active than the standard Uganda one showed that both the initial adsorption and subsequent diffusion were very much slower.

The activity of Uganda soil was not reduced by removal of material soluble in organic solvents, and was only partly reduced by complete extraction of iron compounds.

Variation in temperature over the range 20 to 30°C. had only small effects on the diffusion of DDT and dieldrin within mud blocks.

Repeated applications of DDT and dieldrin to the same blocks did not result in any observable slowing in the rate of disappearance. The concentration of insecticide in the successive layers of mud, did, of course, increase with successive sprayings.

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STUDIES ON AQUEOUS SUSPENSIONS OF INSECTICIDES.

PART VII. THE INFLUENCE OF RELATIVE HUMIDITY UPON THE SORPTION OF INSECTICIDES BY SOILS.

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Contents.

Previous experience has shown that the physical characteristics of an insecticide formulation can play an important part in controlling the relative effectiveness of the insecticide. These are mainly determined during the manufacture of the formulation and so the insecticide can be applied in a form which is likely to provide the best results for any particular control measure. More recently it has become apparent that even when the optimum physical properties have been given to an insecticide deposit its effectiveness can vary at different times after application, apart from any general decline due to evaporation or decomposition or sorption into a substrate.

The general climatic conditions ruling during the time when the effectiveness of the deposits is measured could influence the behaviour of the insect and those factors which control the amount of insecticide which the insect acquires during its period of contact with the deposit. Recently there has been evidence during field trials that the effectiveness of dieldrin used in mud and thatch huts against mosquitos varied with the relative humidity of the air in the huts (Bordas & Navarro, 1955; Burnett, 1956).

A general survey on the influence of temperature and humidity upon the action of insecticides is being made, but in view of these field results, attention was given first of all to the effects of humidity. It was first shown that humidity had no detectable effect upon the kills of mosquitos kept in the range 20 to 95 per cent. after topical applications of DDT, dieldrin, γ BHC or diazinon or after exposure to deposits of wettable powders of DDT, dieldrin or γ BHC (Hadaway & Barlow, 1957). Therefore it would seem most likely that any influence of humidity is upon the availability of the insecticide in the deposit during the exposure period rather than upon the action of the insecticide in the insect.

The nature of the surface sprayed is important in any consideration of insect: insecticide interactions but this paper is concerned with only one type of surface material, the soils used in the construction of houses in many parts of the tropics where malaria control schemes are operated. In Parts III, V and VI of this series the behaviour of suspensions of insecticides sprayed on air-dried soils has

been described (Hadaway & Barlow, 1952, 1955, 1958). Under average laboratory conditions, 25°C. and 50 to 70 per cent. R.H., all the insecticides used, aldrin, γ BHC, dieldrin and DDT, were rapidly sorbed on to the internal surface of the blocks made of air-dried soil and the insecticide particles disappeared from the sprayed surface. The most active soils were of the red lateritic type. This sorption resulted in a very marked reduction in toxicity of the deposits of the insecticides, although aldrin and γ BHC, which have a marked fumigant action, could continue to act by this method. After adsorption, the insecticides diffused slowly away from the sprayed surface. It was noticed that relative humidity had an influence upon the rates at which particles of DDT and γ BHC disappeared. Increasing the humidity reduced the rate of loss. This humidity effect on the sorption of insecticides by soils has now been investigated more fully.

Materials and Methods.

Details of the biological and chemical methods used are described in Part VI (pp. 315–316) of this series (Barlow & Hadaway, 1958). In contact-toxicity tests, mosquitos were confined on the sprayed surface under funnels, but where fumigant action alone was to be measured the funnels were modified so that a metal gauze kept the mosquitos about 0·5 cm. away from the sprayed surface.

For conditioning at different humidities, sprayed blocks were kept either in desiccators over sulphuric acid solutions or in one of two wooden cabinets. One cabinet contained several bowls of water and had a humidity of about 90 per cent., the other contained trays of anhydrous calcium chloride and had a humidity of 30–40 per cent. Cabinets and desiccators were kept in a constant-temperature room at 25°C. The desiccators were used mainly to hold the blocks needed for chemical estimations. The cabinets were needed for the biological tests where it was essential that the mosquitos should be exposed to the blocks under the same conditions as those at which the blocks had been kept previously. The cabinets were large enough to allow the manipulations involved in exposing the mosquitos without too much disturbance of the conditioned air.

The mud blocks were of three sizes: small, 2·1-cm. diameter, were used in some of the measurements on sorption of water vapour; medium, 4·3-cm. diameter, were used in chemical determinations of the distribution of insecticides within the blocks; large, 7·4-cm. diameter, were used for biological tests. All the blocks had the same thickness of about 1·2 cm. A layer of the medium block weighing 0·25 g. had a thickness of about 0·1 mm., and one weighing 4·0 g. had a thickness of 1·7 mm.

The Effect of Humidity upon the Sorption of Dieldrin.

Dieldrin is dealt with first, as this is at present the most important insecticide in the field trials where humidity effects have been noticed. Medium-sized mud blocks were kept at one of three humidities, 10, 50 and 90 per cent., before spraying. They were sprayed with 100 mg. per sq. ft. of a 0–10 micron suspension of dieldrin and returned to their respective desiccators. At intervals they were examined visually and the distribution of the insecticide in the blocks was also determined.

As observed visually, the rate at which the particles of dieldrin disappeared from the sprayed mud decreased with increased humidity. Even in an hour or two there were marked differences in appearance. At 10 per cent. R.H. most of the deposit had gone in a few hours, at 50 per cent. overnight, and at 90 per cent. in a few days. While the differences in rates were strikingly obvious to the eye it was not easy to make quantitative measurements. The difficulty lies in collecting the insecticide particles from the surface of the soil without removing any soil itself. However, it was possible to do this to a large extent with the

adhesive-tape sampling method (Barlow, 1955). Table I gives the recoveries of dieldrin on tape samples from mud blocks kept at 10 per cent. and 90 per cent. R.H.

TABLE I.

Superficial dieldrin deposits on Uganda mud blocks kept in different humidities.

Time after spraying (hr.)	Dieldrin recovered (mg./sq. ft.)	
	10 per cent. R.H.	90 per cent. R.H.
2	68	89
4	37	67
7	30	65
24	10	42

The above figures give some idea of the relative quantities of dieldrin remaining on the surface as particles at different times, although the picture is not as clear as it might be because the tape does remove some of the mud itself. This is shown by the recovery of about 10 per cent. of the dieldrin after 24 hours, when no insecticide was visible on the surface, and by the small differences in

TABLE II.

Average percentage recoveries of dieldrin from successive layers of Uganda mud blocks.

R.H. (%)	Layer no.	Wt. of layer (g.)	Time after spraying			
			1 hour	3 hours	4 days	13 days
10	1	0·25	92	88	69	52
	2	4·0	8	12	31	48
	3	4·0	0	—	0	0
	4	4·0	—	—	—	0
	5	4·0	—	—	—	0
Av. wt. recovered (mg./sq. ft.)			103	96	91	86
50	1	0·25	92	75	17	10
	2	4·0	8	25	79	67
	3	4·0	0	—	4	20
	4	4·0	—	—	0	3
	5	4·0	—	—	—	0
Av. wt. recovered (mg./sq. ft.)			103	88	98	91
90	1	0·25	92	79	16	6
	2	4·0	8	21	37	23
	3	4·0	0	—	27	20
	4	4·0	—	—	20	15
	5	4·0	—	—	—	12
	6	4·0	—	—	—	10
	7	8·0	—	—	—	14
Av. wt. recovered (mg./sq. ft.)			103	96	91	103

the recoveries at 4 and 7 hours. When the insecticide is first sorbed it is concentrated in the outermost layers of mud and consequently even very small amounts of mud contain high concentrations of insecticide.

Once the dieldrin is sorbed, its behaviour can be followed by sectioning the mud blocks at different time intervals and determining the insecticide in each layer. In the previous paper in this series (Barlow & Hadaway, 1958) it was shown that the three insecticides dieldrin, γ BHC and DDT all continue to diffuse further into the blocks after sorption is completed at rates which, under C.T. room conditions, were in the order γ BHC > dieldrin > DDT. It was now found that when the blocks sprayed with dieldrin were kept at different humidities the rate of diffusion increased with increasing humidity as shown by the figures in Table II.

As explained above, there were marked differences in appearance of the blocks a few hours after spraying but this is not shown in the recoveries from the first two layers of mud at 3 hours because most of the sorbed dieldrin is still concentrated in the thinnest outer layer (0·25 g. = 0·1 mm.) regardless of the actual amount that still remains as particles. However, the results shown in Table II clearly indicate that dieldrin once adsorbed then diffuses inwards at a speed which increases with humidity. At 10 per cent. R.H. movement is slow and at 13 days half of the dieldrin is still in the outermost layer, whereas at 90 per cent. R.H. the dieldrin has spread through the blocks.

TABLE III.

Average percentage distribution of dieldrin in Uganda mud blocks after keeping at various humidities.

R.H. (%)	Layer no.	Wt. of layer (g.)	Time in weeks after moving to fresh humidity				
			0	1	2	3	4
10	1	0·25	5	—	6	—	6
	2	4·0	57	—	53	—	54
	3	4·0	29	—	28	—	28
	4	4·0	9	—	10	—	10
	5	4·0	0	—	2	—	3
	6	4·0	0	—	0	—	0
	7	8·0	0	—	0	—	0
Av. wt. recovered (mg./sq. ft.)			98	—	91	—	98
50	1	0·25	5	—	4	—	2
	2	4·0	57	—	48	—	42
	3	4·0	29	—	28	—	27
	4	4·0	9	—	15	—	17
	5	4·0	0	—	5	—	9
	6	4·0	0	—	0	—	2
	7	8·0	0	—	0	—	0
Av. wt. recovered (mg./sq. ft.)			98	—	88	—	99
90	1	0·25	5	3	2	3	2
	2	4·0	57	27	21	17	16
	3	4·0	29	23	20	16	15
	4	4·0	9	18	17	15	15
	5	4·0	0	12	14	13	13
	6	4·0	0	7	11	13	13
	7	8·0	0	10	16	24	27
Av. wt. recovered (mg./sq. ft.)			98	104	94	91	91

The same influence of relative humidity upon the diffusion of sorbed dieldrin was also shown when blocks which had been kept at a given humidity for some time after spraying were transferred to other humidities. Blocks were sprayed with 100 mg. per sq. ft. of 0–10 micron suspension of dieldrin and kept at 50 per cent. R.H. for 23 days. The distribution at this time was measured and the rest of the blocks were divided between three humidities, 10, 50 and 90 per cent. These blocks were sampled at intervals, and the distribution of dieldrin is shown in Table III.

Thus, if a block containing sorbed dieldrin which has been kept at 50 per cent. R.H. is transferred to 10 per cent. R.H., the distribution of dieldrin does not alter over four weeks. If it is kept at 50 per cent., diffusion proceeds slowly. If it is transferred to 90 per cent. R.H., diffusion greatly increases. There is a marked change at one week, and at three to four weeks the concentration is, in the present experiment, approaching uniformity throughout the block.

The changes in distribution on transferring the dieldrin-treated blocks from 50 to 90 per cent. R.H. were striking, even over a period of one week. A further experiment was therefore made in which the behaviour of the insecticide was observed over the first two days after transference. Blocks sprayed with a suspension of 0–10 micron particles of dieldrin at 100 mg. per sq. ft. were kept in desiccators at what was intended to be 50 per cent. R.H. Due to a mistake in the preparation of the sulphuric acid used in the desiccators the actual humidity was about 25 per cent. However, the distribution of dieldrin was determined after three weeks and the experiment continued because, although it did not now fit in exactly with the results shown in Table III, it still served to show how rapidly the distribution alters on moving from a low to a high humidity. The blocks which had therefore been kept at 25 per cent. R.H. for three weeks were now transferred to 90 per cent. R.H. and the dieldrin distribution determined one and two days afterwards. These are given in Table IV. As expected from the previous results, there were large movements of dieldrin even during the first two days at high humidity.

TABLE IV.

Average percentage distribution of dieldrin in Uganda mud blocks after transference from 25 to 90 per cent. R.H.

Layer no.	Wt. of layer (g.)	Time in days after moving to high humidity		
		0	1	2
1	0·25	20	8	3
2	4·0	80	79	61
3	4·0	0	13	29
4	4·0	0	0	7
5	4·0	0	0	0

The field trials mentioned in the introduction suggested that the mortality of mosquitos in treated huts increased as the humidity increased, and this was now confirmed by laboratory tests. In the first experiments, mud blocks which had been sprayed 53 days previously with a commercial dieldrin wettable powder at various dosages or with a 0–10 micron crystalline suspension of dieldrin at 100 mg. per sq. ft. were separated into two groups and kept in cabinets at either 40 or 90 per cent. R.H. for one week. Mosquitos (*Aëdes aegypti* (L.)) were then exposed on the blocks in the cabinets, and the percentage kills are given in

Table V. It can be seen that, with both a suspension of pure dieldrin and with a commercial powder at several dosages, kills were much higher after the blocks had been kept at 90 per cent. than when they had been kept at 40 per cent. R.H.

TABLE V.

The toxicity to *A. aegypti* of dieldrin-treated mud blocks kept at different humidities.

Formulation	Dieldrin dosage (mg./sq. ft.)	R.H. (%)	Percentage kill 24 hr. after exposure of . . . mins.			
			32	64	128	256
Wettable powder ..	100	90	35	100		
		40	0	10	55	
	50	90	0	30	100	
		40			5	45
	25	90			10	50
		40				0
0–10 micron crystalline suspension	100	90	40	100		
		40	0	5	60	

In further tests it was found that the effect of humidity upon the biological activity of the blocks was almost completely reversed in 24 hours. Dieldrin-treated blocks were kept in cabinets for 24 hours at 40 or 90 per cent. R.H., and mosquitos were exposed on them for various times. The blocks were then transferred to the opposite humidity for a further 24 hours and re-tested. The percentage kills are given in Table VI.

TABLE VI.

The effect of changes in relative humidity upon the toxicity of dieldrin-treated mud blocks.

Dosage of dieldrin and age of blocks	Relative humidity conditions	Percentage kill 24 hours after exposure of . . . mins.				
		4	8	16	32	64
0–10 micron suspension, 100 mg./sq. ft. 3 weeks	90% for 24 hr.	55	100	100		
	40% „ 24 „		0	30	68	
	90% transferred to 40% for 24 hr.		0	5	48	
	40% transferred to 90% for 24 hr.	37	65	100		
Commercial 50% wettable powder, 50 mg./sq. ft. 3 weeks	90% for 24 hr.					100
	40% „ 24 „					0
	90% transferred to 40% for 24 hr.					25
	40% transferred to 90% for 24 hr.					100

This effect of humidity was also exerted on blocks at various times after spraying. Mud blocks were sprayed at a dosage of 100 mg. per sq. ft. of 0–10 micron crystals of dieldrin and were stored under C.T. room conditions.

Tests were made 3, 8 and 24 weeks after spraying. Twenty four hours before each test, some blocks were placed in a cabinet at 90 per cent. R.H. and others were placed at 40 per cent. R.H., and mosquitos were then exposed on the blocks in the cabinets so that no changes in humidity occurred during the exposure periods. The percentage kills are given in Table VII.

TABLE VII.

The effect of difference in relative humidity upon the toxicity of dieldrin-treated mud blocks at various times after spraying.

Time after spraying (weeks)	R.H. (%)	Percentage kill 24 hours after exposure of . . . mins.			
		32	64	128	256
3	90	100			
	40	0			
8	90	40	100		
	40	0	5	60	
24	90		0	30	100
	40			0	8

Dieldrin can exert a "fumigant" action during very long exposure periods and the vapour phase action is also influenced by changes in humidity. Thus, the blocks of Table VII, 24 weeks after spraying, gave no kill when the mosquitos were kept at a distance of 0·5 cm. from the mud surface for 16 hours if the humidity was 40 per cent., but gave a kill of 45 per cent. if the humidity during the exposure period was 90 per cent.

The Effect of Humidity upon the Sorption of γ BHC.

Similar experiments were also made with γ BHC. Medium-sized Uganda mud blocks were sprayed at a dosage of 100 mg. per sq. ft. The particle-size distribution was not known as the formulation used was a commercial wettable powder. The recovery of γ BHC was determined for two blocks immediately after spraying while the other blocks were distributed between desiccators having relative humidities of 10, 50 and 90 per cent.

Because of the presence of an inert filler it was not so easy to assess visually the influence of humidity upon the rate of disappearance of particles from the surface of the blocks as it was with the pure suspensions of dieldrin and DDT (pp. 334 & 342). Still, there were obvious differences, a few hours after spraying, between the blocks kept at different humidities and, as with dieldrin, it seemed that the sorption rates decreased as humidity increased.

At various times after spraying, two blocks were taken from each desiccator and the distribution of γ BHC determined. The results are given in Table VIII.

These results with γ BHC show the same pattern as those for dieldrin but even more clearly do they demonstrate the distinctive effects of humidity upon the primary sorption process and on the subsequent diffusion further into the blocks. One day after spraying there was a higher concentration of insecticide in the first layer of mud at 90 per cent. than at 10 per cent. R.H. This was due to the particles which still remained on the surface at the high humidity. The portion which had been sorbed had penetrated further than that at 10 per cent. Once the insecticide was sorbed it diffused rapidly into the block at 90 per cent.

but only very slowly at 10 per cent. R.H. At 50 per cent. R.H. the situation was intermediate between those two extremes.

Blocks sprayed with γ BHC were next kept at the same humidity for two weeks before the distribution of γ BHC was determined. They were then divided into two groups and one was placed at low, the other at high, humidity. It was not thought wise to keep them in desiccators this time because when the insecticide has diffused through the blocks its rate of evaporation to the atmosphere

TABLE VIII.

Average percentage recoveries of γ BHC from successive layers of Uganda mud blocks.

R.H. (%)	Layer no.	Wt. of layer (g.)	Time after spraying (days)				
			0	1	3	7	14
10	1	0·25	92	45	36	25	22
	2	4·0	8	55	64	75	78
	3	4·0	0	0	0	0	0
	4	4·0	—	0	0	0	0
Av. wt. recovered (mg./sq. ft.)			95	100	100	106	107
50	1	0·25	92	22	12	6	4
	2	4·0	8	75	67	53	36
	3	4·0	0	3	19	27	26
	4	4·0	—	0	2	12	17
	5	4·0	—	—	0	3	9
	6	4·0	—	—	0	0	5
	7	8·0	—	—	—	0	4
Av. wt. recovered (mg./sq. ft.)			95	102	100	100	102
90	1	0·25	92	74	47	1	1
	2	4·0	8	17	19	20	16
	3	4·0	0	7	13	17	16
	4	4·0	—	2	8	15	14
	5	4·0	—	0	6	12	15
	6	4·0	—	—	3	11	14
	7	8·0	—	—	5	23	25
Av. wt. recovered (mg./sq. ft.)			95	107	103	78	66

increases (compare Table II in Part VI of this series (Barlow & Hadaway, 1958), and the lower recoveries after 7 and 14 days at 90 per cent. R.H. in Table VIII of this paper). Keeping them in small desiccators might mean that high concentrations of vapour, which would modify their behaviour, would be present around the blocks. The different humidities were therefore maintained in two wooden cabinets and the blocks were placed either in one kept at about 30 per cent. R.H. or in one kept at 90 per cent. R.H. Distributions of insecticides were determined at intervals, and are shown in Table IX.

It can be seen that the results were similar to those obtained with dieldrin in the same kind of experiment. At low humidity, 30 per cent. this time, diffusion of γ BHC was very slow and also there was no detectable loss by evaporation. At high humidity the γ BHC moved rapidly, so that the concentration in the blocks was more or less uniform within about a week. When this condition was achieved the insecticide began to be lost from the blocks quite rapidly. The approximate percentage losses of γ BHC from the blocks at 90 per cent. R.H.

were: 1 week, 20; 2 weeks, 45 and 4 weeks, 80 per cent. That the decreasing recoveries were not due to inability of the solvent to extract the γ BHC from the blocks at 90 per cent. R.H., when they contain a high percentage of water, was shown by the following considerations and experiments. Both dieldrin and DDT, which suffer negligible loss by evaporation, were recovered completely from

TABLE IX.

Average percentage distribution of γ BHC in Uganda mud blocks after transference to different humidities.

R.H. (%)	Layer no.	Wt. of layer (g.)	Time (weeks) after transference to different humidity			
			0	1	2	4
30	1	0·25	1	1	2	2
	2	4·0	33	34	33	32
	3	4·0	27	24	22	22
	4	4·0	19	18	16	16
	5	4·0	11	11	11	11
	6	4·0	5	6	7	7
	7	8·0	5	7	10	11
Av. wt. recovered (mg./sq. ft.)			94	93	112	105
90	1	0·25	1	0	1	0
	2	4·0	33	18	13	12
	3	4·0	27	16	14	12
	4	4·0	19	17	13	12
	5	4·0	11	15	13	12
	6	4·0	5	13	13	14
	7	8·0	5	21	32	38
Av. wt. recovered (mg./sq. ft.)			94	74	52	17

blocks kept at 90 per cent. Equilibrium in the sorption of water vapour by the blocks was achieved in a few days and so the water content of these blocks was constant during the time that the recoveries of γ BHC were decreasing. Some blocks kept at 90 per cent. humidity for four weeks were dehydrated by placing at 0 per cent. R.H. for 24 hours before extracting. They gave the same recoveries as blocks which were not so treated.

The percentage recoveries of γ BHC in the lowest layer of each block at 90 per cent. R.H. at two and four weeks were noticeably greater than would be expected for uniform concentration throughout the blocks. This was almost certainly due to the blocks being placed flat on a small wooden platform in the cabinets, thereby impeding the diffusion of vapour away from the lower surface. This feature also provided further evidence that the reductions in recovery were due to evaporation of the insecticide.

Tests of the biological activity of blocks sprayed with γ BHC were also made at different humidities. Blocks sprayed with γ BHC at 100 mg. per sq. ft. two weeks previously were divided into two groups, one being placed at 35 per cent. and the other at 90 per cent. R.H. for 24 hours. Mosquitos were exposed to them in two ways; directly on the blocks, which gave mixed contact and fumigant action (although almost certainly it was mainly the former because of the short exposure used), and by keeping them 0·5 cm. away from the mud surface to give fumigant action alone.

After the exposures, the groups of mud blocks were placed for 24 hours at the opposite humidity to that which they had previously experienced and were retested. All the exposures of mosquitos were, of course, made in the cabinets at the humidities to which the blocks had been acclimatised during the previous 24 hours. Results are given in Tables X and XI.

TABLE X.

The effect of changes in relative humidity upon the mortalities of mosquitos exposed directly to mud blocks treated with γ BHC.

Relative humidity conditions	Percentage kill 24 hr. after exposure of . . . mins.				
	2	4	8	16	32
90% for 24 hr.	14	65	95	100	
35% ,, ,, ,, ...			0	0	0
90% transferred to 35% for 24 hr.				0	0
35% ,, ,, 90% ,, 24 ,,	0	35	85	100	

Thus both the contact and fumigant actions of blocks treated with γ BHC increased in effectiveness with increased humidity and this change was reversible.

TABLE XI.

The effect of changes in relative humidity upon the mortalities of mosquitos exposed to the fumigant action of blocks treated with γ BHC.

Relative humidity conditions	Percentage kill 24 hr. after exposure of . . . mins.		
	30	60	120
90% for 24 hr.	32	100	
35% ,, ,, ,, ...		0	0
90% transferred to 35% for 24 hr.		0	0
35% ,, ,, 90% ,, 24 ,,	17	100	

The Effect of Humidity upon the Sorption of p,p′DDT.

Quantitative determinations of the effect of humidity upon the distribution of sorbed DDT were also made. Medium-size Uganda mud blocks were sprayed with 100 mg. per sq. ft. of a 0–10 micron suspension of p,p′DDT. The recovery of insecticide was measured on two blocks and the rest were divided into three groups which were placed in desiccators at 10, 50 or 90 per cent. R.H. Blocks were sampled at different times after spraying.

As judged visually, the rate of sorption again bore an inverse relationship to humidity. Five hours after spraying, there was an obvious gradation, the amount of surface deposit decreasing from 90 to 50 to 10 per cent. R.H. At 24 hours, there was very little deposit left at 10 per cent., a moderate one at 50 per cent., and a heavy one at 90 per cent. R.H. Even at 28 days, long after the surface

deposit had disappeared on blocks at 10 and 50 per cent. R.H., a heavy deposit remained on those kept at 90 per cent. These external differences in appearance of the blocks were in agreement with the measurements of distribution at various times which are shown in Table XII.

TABLE XII.

Average percentage recoveries of p,p′DDT from successive layers of mud blocks kept at different humidities.

R.H. (%)	Layer no.	Wt. of layer (g.)	Time after spraying (days) 0	5	6	28
10	1	0·25	93	86	37	26
	2	4·0	6	14	63	73
	3	4·0	1	0	0	1
	4	4·0	0	0	0	0
Av. wt. recovered (mg./sq. ft.)			89	100	93	103
50	1	0·25	93	87	15	10
	2	4·0	6	13	63	39
	3	4·0	1	—	18	21
	4	4·0	0	—	4	14
	5	4·0	—	—	0	9
	6	4·0	—	—	—	5
	7	8·0	—	—	—	3
Av. wt. recovered (mg./sq. ft.)			89	100	100	92
90	1	0·25	93	95	84	79
	2	4·0	6	5	9	6
	3	4·0	1	0	4	3
	4	4·0	0	—	3	3
	5	4·0	—	—	—	3
	6	4·0	—	—	—	3
	7	8·0	—	—	—	3
Av. wt. recovered (mg./sq. ft.)			89	105	91	98

Again, as with dieldrin and γ BHC, whereas the rate of the initial sorption process was increased by decreasing humidity the rate of diffusion of the sorbed DDT inwards was hindered. At 90 per cent. R.H., sorption was very slow but the 20 per cent. or so of DDT which was sorbed in four weeks had penetrated right through the block. Some of these blocks were kept for 16 weeks, at which time there were still marked traces of the deposit to be seen on the surface. Analysis showed that about 80 per cent. of the DDT had been sorbed and was uniformly distributed through the blocks.

The influence of changes in humidity upon the distributions of DDT already sorbed was next measured. Blocks sprayed with 100 mg. per sq. ft. of a suspension of p,p′DDT were kept at 50 per cent. R.H. for 28 days. Two blocks were then sampled to show the distribution of insecticide at this time and the rest were divided between desiccators at 10, 50 and 90 per cent. R.H. Distributions were determined at different times afterwards and are shown in Table XIII.

The DDT in the blocks at 10 and 50 per cent. R.H. behaved as expected. There was little change in the distribution at 10 per cent. and a slow diffusion at 50 per cent. At 90 per cent., however, there occurred the unexpected phenomenon of movement of the insecticide back into the surface layers of mud.

This reverse movement was rapid, as it happened within the first week, and thereafter for seven more weeks the concentration in the thin outer layer remained the same. On the other hand, the part of the insecticide which did not behave in this abnormal way continued to diffuse further inwards—the usual effect of high humidity. As this was the only exception in the general plan of the behaviour of all three insecticides in Uganda mud, further experiments were carried out.

TABLE XIII.

Average percentage distribution of p,p′DDT in mud blocks after transference to different humidities.

R.H. (%)	Layer no.	Wt. of layer (g.)	Time (weeks) after transference to different humidity			
			0	1	4	8
10	1	0·25	10		8	7
	2	4·0	60		58	63
	3	4·0	22		21	21
	4	4·0	8		8	7
	5	4·0	0		3	1
	6	4·0	—		1	0
	7	8·0	—		1	0
Av. wt. recovered (mg./sq. ft.)			91		98	92
50	1	0·25	10		5	5
	2	4·0	60		44	38
	3	4·0	22		24	24
	4	4·0	8		14	15
	5	4·0	0		7	9
	6	4·0	—		3	5
	7	8·0	—		3	4
Av. wt. recovered (mg./sq. ft.)			91		93	94
90	1	0·25	10	31	32	30
	2	4·0	60	30	29	21
	3	4·0	22	17	8	9
	4	4·0	8	13	7	9
	5	4·0	0	7	6	8
	6	4·0	—	2	5	8
	7	8·0	—	0	12	15
Av. wt. recovered (mg./sq. ft.)			91	94	111	91

This time, blocks sprayed with 100 mg. per sq. ft. of p,p′DDT were kept at 50 per cent. R.H. for four weeks. The distribution at this time was measured and the remaining blocks transferred to either 50, 80 or 90 per cent. R.H. as it was known that DDT behaved normally at 10 per cent. and it was of interest to see what happened at a humidity such as 80 per cent. Table XIV shows the position of the DDT at different times afterwards.

At 90 per cent. R.H., the DDT again showed exceptional behaviour although the amount of DDT returning to the outer layer was not so great as in the previous experiment. Once there, this "abnormal" fraction remained during six weeks. Again this agreed with the results given in Table XIII. DDT at 80 per cent. R.H., however, behaved as the other insecticides had done at higher

humidities in that the DDT already sorbed when the humidity was changed continued to diffuse further inwards at an appreciable rate. The "abnormal" behaviour of DDT at 90 per cent. R.H. was shown to be reversible by moving two blocks kept at 90 per cent. R.H. to 50 per cent. R.H. 11 days before the

TABLE XIV.

Average percentage distribution of p,p′DDT in mud blocks after transference to different humidities.

R.H. (%)	Layer no.	Wt. of layer (g.)	Time (weeks) after transference to different humidities			
			0	1	3	6
50	1	0·25	10	8	8	6
	2	4·0	62	59	51	42
	3	4·0	19	20	21	22
	4	4·0	6	8	11	13
	5	4·0	2	3	5	8
	6	4·0	0	1	2	4
	7	8·0	0	1	2	5
Av. wt. recovered (mg./sq. ft.)			92	116	91	101
80	1	0·25	10	9	9	9
	2	4·0	62	43	32	20
	3	4·0	19	20	19	17
	4	4·0	6	11	14	14
	5	4·0	2	7	10	13
	6	4·0	0	6	7	10
	7	8·0	0	5	9	18
Av. wt. recovered (mg./sq. ft.)			92	110	97	98
90	1	0·25	10	24	24	25
	2	4·0	62	44	44	42
	3	4·0	19	11	9	8
	4	4·0	6	9	6	6
	5	4·0	2	6	5	5
	6	4·0	0	3	4	5
	7	8·0	0	3	7	9
Av. wt. recovered (mg./sq. ft.)			92	114	117	89

final sampling at six weeks. At six weeks the distribution in these blocks was as follows:

Layer no.	1	2	3	4	5	6	7
DDT (%)	7	48	17	7	6	6	9

The increased concentration of DDT had reverted to the second layers of the blocks and was already diffusing further inwards.

This peculiar behaviour of DDT at high humidities was thus confirmed. It has remained as an exception to the general and consistent pattern shown by the influence of humidity on the sorption and diffusion of insecticides in Uganda mud blocks.

A few observations were made on the biological activity of DDT-treated blocks. They had been sprayed with 0–10 micron crystals of DDT, at 100 mg. per sq. ft., three weeks previously and stored under C.T. room conditions.

Before mosquitos were exposed to them, some blocks were kept at 40 per cent. R.H. and some at 90 per cent. R.H. for 48 hours. After testing, the blocks were transferred to the opposite humidity for a further 48 hours and retested. It can be seen from the percentage kills given in Table XV that the biological activity of the blocks was influenced by changes in humidity. Again, as with dieldrin and γ BHC, increased humidity resulted in increased kills and the effect was reversible.

TABLE XV.

The effect of changes in relative humidity upon the mortalities of mosquitos exposed to DDT-treated mud blocks.

Relative humidity conditions	Percentage kill 24 hr. after exposure of . . . mins.	
	64	128
90% for 48 hr.	13	100
40% „ „ „	0	0
90% transferred to 40% for 48 hr.	0	0
40% „ „ 90% „ 48 „	8	98

The Sorption of Water Vapour by Uganda Soil.

The biological activities of all three insecticides sorbed on Uganda mud blocks were therefore controlled by the relative humidity conditions under which the blocks were kept and, consequently, upon the amount of water sorbed by the mud. The next step, therefore, was to see what the different biological activity corresponded to in terms of water content of the blocks.

Four small blocks, of the size used for carbon tetrachloride sorption tests (Barlow & Hadaway, 1955), were kept in a desiccator over concentrated sulphuric acid until losses in weight had ceased. They were now considered to be free from water vapour. Next they were placed in a desiccator containing a sulphuric acid solution chosen to give 10 per cent. R.H. and were weighed at intervals until their weights were constant. This procedure was repeated at successively higher levels of humidity up to 100 per cent. At the lower humidities, equilibrium was attained rapidly but the time increased at the higher ones until, at 100 per cent., about 15 days were required before weight increases were sufficiently small to be disregarded. The temperature throughout the determinations was 25 ± 1°C. The increases in weight at different humidities are given in Table XVI and are plotted in fig. 1.

TABLE XVI.

Percentage increase in weight of mud blocks exposed to a rising scale of relative humidities.

Per cent. R.H.	10	20	40	60	80	90	100
Per cent. increase over weight at 0% R.H.	0·4	0·8	1·3	1·8	3·2	5·5	17·0

It can be seen that the uptake of water was virtually linear up to about 60 per cent. R.H. and thereafter increased very rapidly. This suggests that, over the linear portion of the curve, water molecules were being sorbed as thin films on the internal surfaces of the blocks but when the vapour pressure became sufficiently high, at more than 70 per cent. R.H., capillary condensation began

to occur at a rapidly increasing rate and pores below a certain diameter became filled with liquid water. This shape of curve is frequently given by water vapour on porous solids. That condensation was occurring was also suggested by measurements of the sorption of benzene and carbon tetrachloride at their saturated vapour pressures on the same blocks. These vapours were sorbed more

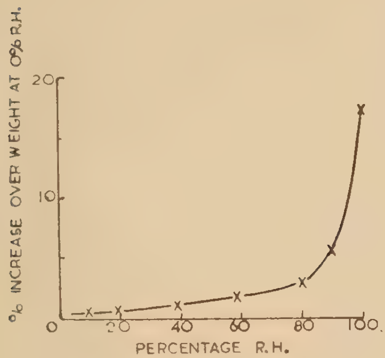

Fig. 1.—Sorption of water vapour at different humidities.

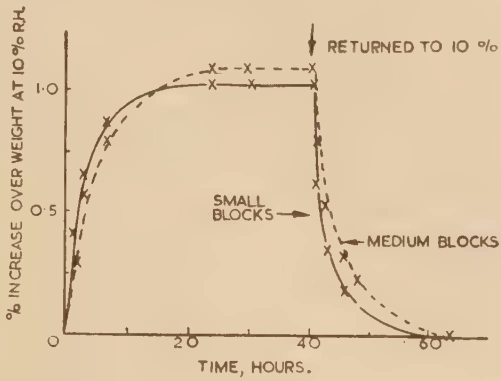

Fig. 2.—Rate of sorption and desorption of water vapour on transferring from 10% to 60% R.H. and back again.

rapidly than water and the maximum percentage weight increases of the blocks were 14·3 and 24·8 per cent. for benzene and carbon tetrachloride, respectively. If these weights are divided by the corresponding liquid densities, the percentages by volume sorbed of water, benzene and carbon tetrachloride were 17·0, 16·3 and 15·5, respectively. These figures are in sufficient agreement to suggest that capillary condensation was occurring in each case and the limiting factor was the size of the capillaries.

It was also of interest to know how quickly the water contents of the blocks responded to changes in humidity and whether these could be correlated with the rates of change of biological activity. This was done in a series of experiments the results of which are shown graphically in figs. 2 to 6.

The first measurements were made in desiccators containing sulphuric acid solutions to give the required humidities. It was already known that equilibrium was reached only slowly at high humidity so the first determinations were made by keeping small and medium blocks at 10 per cent. R.H. until their weights were constant and then moving them to 60 per cent. R.H. This range covered the straight portion of the graph shown in fig. 1. The blocks were weighed at intervals until their weights were constant, after which they were returned to 10 per cent. R.H. and the weighings continued. Uptake of water vapour was complete in 24 hours in both sizes of block (fig. 2). Although the medium blocks lagged behind the small in the early stages they eventually took up a rather greater weight of water. Desorption was rapid and complete in 24 hours. This experiment was repeated but the sorption-desorption cycle was now over the range 30 to 90 per cent. R.H. which includes the region where capillary condensation occurs and was also approximately equal to that used in the biological tests. As expected, the blocks took longer to reach equilibrium over this range, sorption in fact taking about 72 hours for completion. Desorption, however, was faster and finished in about 24 hours. Again the medium lagged behind the small blocks and again they took up rather more water vapour, as shown in fig. 3.

Further experiments were done with three sizes of mud blocks in the two cabinets used for biological tests. One cabinet had a humidity of 30 to 40 per cent. during the test period, the other one of 90 per cent. Small, medium and large blocks were stood upright in the cabinets so that the water vapour could diffuse in and out of the blocks at both main surfaces. Sorption was complete

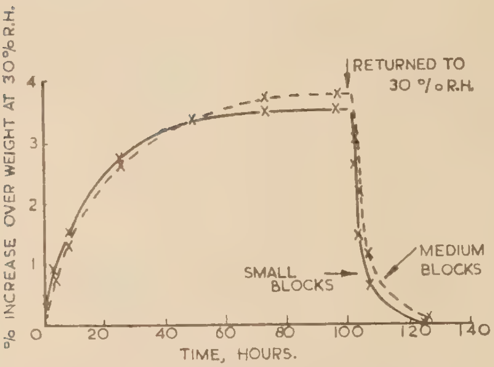

Fig. 3.—Rate of sorption and desorption of water vapour on transferring from 30% to 90% R.H. and back again.

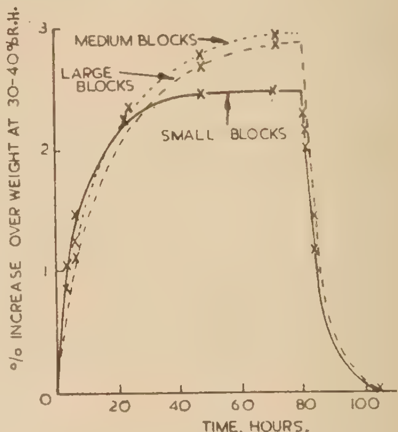

Fig. 4.—Rate of sorption and desorption of water vapour on transferring from 30–40% to about 90% R.H. and back again.

in the small blocks in 48 hours but not quite complete in 72 hours in the medium and large blocks (fig. 4). Desorption was rapid from all three sizes and was complete in 24 hours. Therefore, although the three sizes of blocks were of uniform thickness they did show some small quantitative differences in sorption of vapour. However, in general, the sorption of water vapour was a function of the mud itself and was not influenced unduly by the size of the blocks used in the tests.

Therefore, some determinations of biological activity were now made on large blocks which had been sprayed with a 0–10 micron suspension of dieldrin, at 100 mg. per sq. ft., 23 days previously. These were placed in the low-humidity cabinet for 24 hours, after which time mosquitos were exposed on them. They

TABLE XVII.

The rate of change of biological activity after transferring dieldrin-treated mud blocks from a low to a high humidity.

Humidity conditions	Time (hr.) after transfer to 90% R.H.	Percentage kill 24 hr. after exposure of . . . min.			
		32	64	96	128
35% R.H.	—		0	0	0
90% R.H.	6		0	0	15
	24		23	68	98
	48	15	65	88	
	72	0	40	80	

were then moved to the 90 per cent. cabinet in which they were stood on edge in a rack, being thus treated in exactly the same way as the blocks used for the measurements of water sorption. At intervals the blocks were laid flat and mosquitos exposed to them. The kills obtained are given in Table XVII.

Median lethal exposure times were determined very roughly from these results, and fig. 5 shows a graph of the change of these exposure times with times after transference to 90 per cent. R.H. compared with sorption of water vapour by the same sized blocks in the same cabinet. It is clear that the rate of change of biological activity is very similar to that of sorption of water vapour during the first 48 hours. The reduction in kill at 72 hours is almost certainly due to reduction in surface concentration of dieldrin caused by the accelerated diffusion of insecticide further in the blocks which occurs at prolonged high humidities.

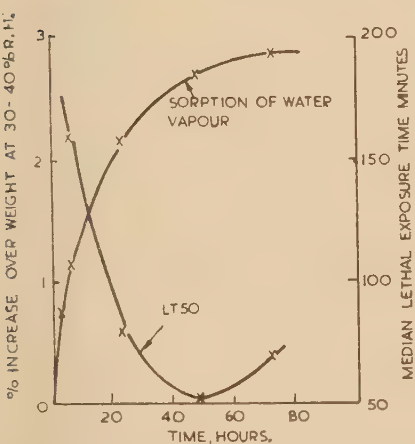

Fig. 5.—Rate of sorption of water vapour on transferring from 30–40% to about 90% R.H. as compared with biological activity of the same blocks.

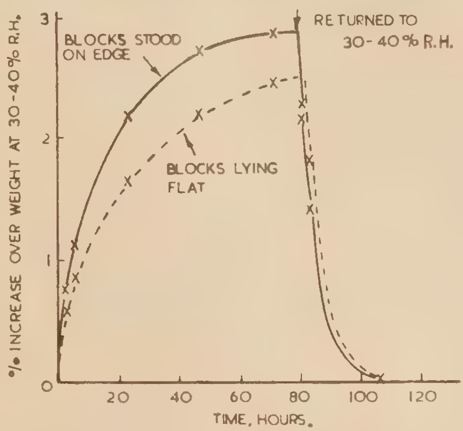

Fig. 6.—The effect of hindering diffusion of water vapour from one surface of the block on the rate of sorption and desorption.

During the cabinet tests a comparison was also made of the rate of sorption and desorption of water vapour between the large blocks stood upright in the usual way and ones which were lying flat on a wooden platform. As expected, the rate of sorption was much slower with the blocks lying flat, although desorption occurred at about the same rate with both groups (fig. 6). It is likely, therefore, that changes in the water content of a mud wall would lag several days behind a sudden increase in humidity, to around 90 per cent., of the air with which the wall was in contact. Most of the changes in biological activity of a treated wall, however, should still occur within about 48 hours of the change.

The Influence of Humidity upon the Sorption of DDT and Dieldrin on other Soils.

In order to see how general this humidity effect was, some visual observations were made on the rate of disappearance of DDT and dieldrin particles sprayed on blocks made from a collection of ten soils. These soils, which included the standard Uganda one, exhibited a range of sorptive activity against the usual 0–10 micron DDT deposit when kept at room conditions of 25°C. and 60 to 70 per cent. R.H. None was completely inactive. Four small blocks were made from each soil, and two of these were sprayed with a 0–10 micron suspension of

DDT at 100 mg. per sq. ft. while the other two were treated with a similar suspension and dosage of dieldrin. One block of each pair sprayed with the same insecticide was kept at 10 per cent. R.H. and the other at 90 per cent. R.H. The blocks were examined daily for the first few days and weekly thereafter. It is difficult to describe all the visual, qualitative observations in detail, but, briefly, humidity showed a strong influence upon the rates of sorption of the two insecticides with all soils. Table XVIII gives some idea of the different responses of the blocks by indicating the times required for complete disappearance of the surface deposits.

TABLE XVIII.

The influence of humidity upon the sorption of DDT and dieldrin by different soils. Times required for complete disappearance of surface deposits.

Soils arranged in order of "activity"	Dieldrin		DDT	
	10% R.H.	90% R.H.	10% R.H.	90% R.H.
Uganda, standard ..	<1 day	2–3 days	1–2 days	some loss at 7 weeks
Entebbe, Uganda, red ..	,,	,,	,,	,, ,, ,, ,,
Jamaica, red	,,	14–21 days	,,	No apparent loss in 7 weeks
Lagos, Nigeria, red ..	,,	,,	,,	,, ,, ,,
Taveta, Kenya, brown ..	,,	28–35 days	,,	,, ,, ,,
Jamaica, grey	,,	No apparent loss in 7 weeks	,,	,, ,, ,,
Babati, Kenya, red ..	,,	,,	,,	,, ,, ,,
Taveta, Kenya, grey-brown	1–2 days	,,	2–3 days	,, ,, ,,
Taveta, Kenya, red ..	,,	,,	1–2 days	,, ,, ,,
New Delhi, India, grey	3–4 days	,,	3–4 days	,, ,, ,,

Just how much relative influence the two humidities chosen had on any particular soil depended upon how active the soil was, as assessed under normal C.T. room conditions, and upon whether dieldrin or DDT was being considered. In accordance with previous experience, dieldrin was sorbed more rapidly than DDT on all the soils under any given conditions.

The times given in Table XVIII, however, are not very sensitive indicators of soil activities and if the blocks were examined at a suitably chosen time a much wider range of activity was visible than is suggested. Thus, at 10 per cent. R.H. a few hours after spraying, the soils showed a wide range of activity, as indicated by the apparent amounts of deposit remaining, against both dieldrin and DDT. After one day, dieldrin had gone from the surface of most of the blocks, and the same was true for DDT after two days. The least active soils took rather longer to sorb the insecticides but, after four days, no deposits were left on the blocks kept at the low humidity. At 90 per cent. R.H., only the more active soils had any effect on the insecticides. The two most active soils were able to sorb dieldrin in 2–3 days even at 90 per cent. whereas there was only a partial loss of DDT on the same blocks in seven weeks. Dieldrin disappeared on the three next most active soils by five weeks while the remainder still had heavy deposits at seven weeks when the experiment was ended. On all but the two most active soils there was little indication of DDT sorption at 90 per cent. R.H.

All the blocks kept at high humidity which still had heavy deposits at seven weeks after spraying were finally transferred to 10 per cent. R.H. The deposits disappeared in their usual order and all had gone in five days.

Finally, it should be mentioned that there was no correlation between the ability of the soils to sorb insecticides and their ability to sorb water.

Discussion.

It is evident from the foregoing results that changes in relative humidity can have a very pronounced effect upon the biological activity of insecticides such as γ BHC, dieldrin and DDT during and after sorption on to soils. Therefore, if the insecticides under actual field conditions are in the sorbed state, these laboratory experiments support and provide an explanation for the influence of humidity on mosquito mortality which has been observed in the field.

Biologically, in both laboratory and field, the picture is a simple one. An increase in humidity is followed by an increase in the insecticidal effectiveness of deposits of dieldrin and γ BHC and DDT on mud blocks (this paper), of dieldrin and γ BHC on walls and on mud blocks (Bordas & Navarro, 1955) and dieldrin on mud walls (Burnett, 1956). The biological tests also show that both contact and fumigant action, where this is possible, are influenced in this way. This change in activity of the deposits is reversible and a reduction in humidity is followed by a reduction in mortalities of mosquitos entering the huts or in contact with the laboratory blocks.

When, however, an attempt is made to find a reason for this change by seeing what the deposits of insecticides are actually doing when kept under different humidity conditions the picture becomes more complicated, as the experimental results in this paper show.

There are two separate phases in the sorption process on active soils. In the first the insecticide molecules move from crystals lying on the surface of the wall or block to the internal surface of the superficial layers of mud when they are adsorbed. Visually the crystalline particles of insecticide disappear. The length of time spent in this phase was found to be inversely related to humidity. As humidity was increased the rate of initial sorption decreased for dieldrin, γ BHC and DDT. As the insecticides are more readily available to insects as particles lying on the mud surface than in the sorbed condition the biological activities remain at higher levels for longer periods at higher humidities. Whether this is of practical importance depends upon the insecticide in question, the activity of the soil forming the wall and the actual level of humidity. Thus, although the residual lives as particles of all three insecticides were prolonged at 90 per cent. R.H. on the active Uganda mud used in this experiment, γ BHC and dieldrin still disappeared within a few days. DDT, on the other hand, remained as a surface deposit for many weeks at this humidity, whereas at, say, 50 per cent. R.H. it was sorbed in a few days. On less active soils, dieldrin also had a very long life at 90 per cent. R.H. compared with that at lower humidities. However, it is unlikely that the influence of humidity observed in field trials can be concerned with this stage of sorption because it was characterised by reversible increases in kill on changing from low to high humidity. The primary sorption process is irreversible—the particulate deposit cannot be reconstituted.

The second stage consists of the diffusion of the insecticides further into the sprayed walls or blocks. The rates of diffusion were directly related to humidity for the three insecticides on Uganda mud. For example, dieldrin hardly changed its distribution in four weeks when kept at 10 per cent. R.H. At 50 per cent. there was slow diffusion, and at 90 per cent. R.H. rapid diffusion in the same time. Thus in four weeks at 90 per cent. R.H. a uniform concentration was achieved throughout the experimental blocks (see Table III). This situation would have been reached in 12 months or more at 50 per cent. R.H. Gamma BHC behaved in the same way, with the added complication that desorption became rapid once the condition of uniform concentration was being approached, and in four weeks about 80 per cent. of this insecticide had been lost by evaporation (see Table IX). There was no loss at 30 per cent. R.H. where the diffusion rate had been very slow. DDT, in general, behaved similarly, with the exception that when the humidity was raised from 50 to 90 per cent. R.H. there was an

apparent movement of sorbed insecticide back into the outermost layers of mud towards the sprayed surface. The " abnormal " fraction stayed in the outer layer of mud for the eight weeks that the experiment lasted. The remainder of the DDT behaved normally and spread itself uniformly through the rest of the blocks. At 80 per cent. R.H., this peculiarity of DDT was not observed and the behaviour at 90 per cent. remains an exception to the pattern shown by all three insecticides kept at different humidities after spraying on to Uganda mud. In any case the more striking field observations have been made in houses treated with γ BHC and dieldrin.

The general increase in biological activity of the sorbed insecticides at high humidities is not due, therefore, to an increase in concentration in the surface layers of the mud. In fact, high humidities favour diffusion inwards and a decrease in concentration in surface layers. Also, the reversible nature of the changes in biological activity and the rate at which they occur suggest that changes in concentrations of insecticides are not of primary importance in the humidity effect; concentration changes occur more slowly and are not reversible. However, for kills of mosquitos resting on the surface for a given period to be higher at higher humidities, the insects must acquire a greater amount of insecticide. They can do this only if the rate of diffusion of insecticide from mud to insect is greater at high than at low humidities for a given concentration of insecticide. It is already known that this is just the influence which humidity exerts upon diffusion of insecticides further into the sprayed mud blocks, and therefore it would seem that acceleration of diffusion over the internal surface of the mud is accompanied by acceleration of diffusion on to and into objects such as insects which are resting on the mud surface. In other words the mobility of the insecticide molecules sorbed on the mud is presumably controlled by the amount of water vapour also sorbed and this, in turn, depends upon humidity.

It was obviously necessary to have some measurements of how rapidly the water content of the mud blocks varied with changes in humidity and if biological activity changed at a similar rate. The sorption of water vapour by Uganda mud blocks was first measured at a series of relative humidities and, consequently, vapour pressures of water. Adequate time was allowed for equilibrium to be reached at each humidity. Up to about 60 per cent. R.H. the uptake of water was linear but thereafter it increased rapidly and at the higher humidities capillary condensation was probably occurring. Next, the rates of sorption and desorption over certain ranges of humidity were found. Over the linear portion of the sorption isotherm, equilibrium was reached within 24 hours, whereas at higher humidities sorption took longer. At 90 per cent. R.H., for instance, about three days were needed. Desorption, however, was rapid. In the biological tests, dieldrin-treated blocks were kept at 30 to 40 per cent. and then transferred to 90 per cent. R.H. The biological activity changed during the first two days at about the same rate as the water vapour was being taken up by the blocks. On the third day, the biological activity decreased a little but this was almost certainly due to decrease in concentration of insecticide near the sprayed surface following the greater diffusion further into the blocks which occurs at high humidities. It may be said therefore that for any given concentration of an insecticide sorbed on mud with which an insect is in contact the toxicity will vary directly with the water content of the mud and therefore with humidity. If high humidities are prolonged, however, some allowance must be made for the changes in concentration of insecticides which are also controlled by humidity.

While most of the work was done with a single sample of Uganda soil, humidity was also found to influence the sorption of dieldrin and DDT by a range of soils in the same way. Both dieldrin and DDT were sorbed rapidly on all the soils at 10 per cent. R.H., but only dieldrin on the most active at 90 per cent. R.H. and even then the rate was much slower than at the lower humidity.

In the field, therefore, it is evident that the toxicity at any given moment of a mud surface sprayed with an insecticide will depend upon humidity in two ways. In the first place the humidity conditions during the time between spraying and testing will determine how much of the insecticide is sorbed and, of the fraction that is sorbed, how much will remain in the layers of mud nearest to the sprayed surface. Assuming that sorption is complete, the concentration of insecticide in the mud will then give a kill of insects which is controlled by the humidity at the time of exposure. For example, if dieldrin is sprayed on to an active soil, all will be sorbed in a few days, rapidly at low humidity, more slowly at high humidity. If the low humidity persists, diffusion of dieldrin deeper into the mud will be slow, whereas at high humidity it will be fast. At any given time the biological activity, determined at the humidity at which the mud has been kept, will be less at low humidity than at high because the greater potency at high humidity during the test period will more than offset the decreased concentration of insecticide in surface layers. However, if the humidity suddenly increases, the biological effectiveness of the mud will be greater than if it had been kept under high humidity conditions from the beginning. This, of course, is because of the greater concentration of dieldrin in the mud near the insects. In the same way, if a mud which has been in a high humidity is moved to a low humidity it will be less effective than if it had been kept at the same low humidity all the time because the concentration of dieldrin in the surface layers of this mud would be lower. An experiment was made which confirmed these expectations. Uganda mud blocks were sprayed with 150 mg. per sq. ft. of a 0–10 micron suspension of dieldrin (100 mg. per sq. ft. was intended but an error in calibration of the spray tower resulted in the higher dosage). The blocks were divided into two groups, one being kept at 30 per cent. and the other at 90 per cent. R.H. Mosquitos were exposed on the blocks at the humidities at which they had been stored for 12 weeks. The blocks were then transferred to the opposite humidity for 24 hours, and mosquitos were exposed on them at the new humidities. The percentage kills are shown in Table XIX.

TABLE XIX.

The toxicity to *A. aegypti* of dieldrin-treated Uganda mud blocks kept at different humidities.

Humidity conditions	Time	Percentage kill 24 hr. after exposure of . . . mins.						
		2	4	8	16	32	64	128
90%	12 weeks		5	55	98			
Transferred to 30% for 24 hr.							0	0
30%	12 weeks					0	20	63
Transferred to 90% for 24 hr.		5	28	75	100			

It has been previously shown (Barlow & Hadaway, 1958) that the sorption of γ BHC on active soils is beneficial in that the residual life of the insecticide is prolonged. No loss of γ BHC from the standard Uganda soil appeared to occur until the concentration was more or less uniform throughout the blocks, but when this state was reached evaporation took place fairly rapidly. As the diffusion of insecticide proceeds more rapidly at high humidities, it is clear that the residual life of γ BHC on mud will depend upon humidity conditions. At a high humidity a high biological activity for a relatively short time would be

expected, whereas at a low humidity a low biological activity for a much longer time would be expected.

The final physical picture is therefore as follows. Relative humidity controls the amount of water vapour sorbed on the mud. Water vapour appears to be able to retard the sorption of insecticide or to displace insecticide which is already sorbed. Therefore the rate of primary sorption depends upon the amount of water vapour already on the active surface. If there is a small amount of water the rate is fast, if a lot, the rate is slow. After sorption is complete the insecticide is strongly sorbed in the superficial layers of mud at low humidity and diffusion rates are low, whereas, if the amount of sorbed water vapour is increased, it displaces the insecticide. The insecticide is then more mobile and diffuses rapidly because resorption is rendered more difficult by the presence of large amounts of sorbed water.

Summary.

Changes in relative humidity had a very marked influence upon the biological activities of γ BHC, dieldrin and DDT sorbed on Uganda mud blocks. In agreement with field observations, kills of mosquitos increased as the humidity increased and this effect was rapidly reversible.

Disappearance of insecticide particles from the mud surface was inversely related to humidity, the rate increasing as humidity decreased. On the other hand, the rates of diffusion of sorbed insecticide away from the surface were greater at higher humidities.

It is suggested, therefore, that when the biological activity of a mud surface is increased by increasing the humidity, the insects acquire a greater dose of insecticide not because the concentration of insecticide in the surface layers is greater but because the insecticide that is already present acquires a greater mobility. This greater mobility results in a more rapid diffusion in the mud itself away from the treated surface and a greater potential for diffusion into insects resting on the mud surface.

Support for these conclusions was obtained by showing that on transferring dieldrin-treated mud blocks from low to high humidity the change in biological activity occurred at about the same rate as the increase in water content of the blocks.

The influence of humidity upon the sorption of DDT and dieldrin on a selection of soil samples of widely differing origin was observed. Both insecticides disappeared from the surface more rapidly at low than at high humidity on all the soils.

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OBSERVATIONS ON OVIPOSITION IN THE WHEAT BULB FLY, *LEPTOHYLEMYIA COARCTATA* (FALL.).

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Our knowledge of oviposition in the Wheat Bulb Fly, *Leptohylemyia coarctata* (Fall.), in the field has been largely inferred from laboratory observations on the fly and field observations on stages other than the adult. Direct observation on the fly in the field presents considerable difficulty because of its relatively small size, speed of flight and dun colour. It is not surprising therefore that, although looked for, no oviposition in the field has been seen. Gough (1946) reports a similar failure to observe oviposition in the field during the hours of daylight. Flies have been observed to alight on the leaves of potato and sugar-beet and to run down the stems to soil level, but on such occasions it has not been possible to make a closer observation without disturbing them. In view of the limitations associated with field observations, a study of oviposition was begun in the laboratory.

Technique.

In the first series of experiments in 1954, freshly captured females from the field were set up at the rate of 20 per cage. The cages consisted of lamp glasses fitted with a black nylon mesh screen at the bottom and covered on top with muslin from which three feeding tubes containing diluted sweetened condensed

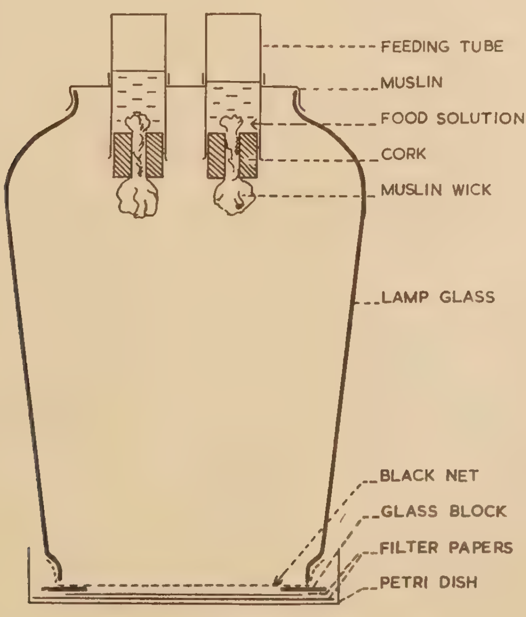

Fig. 1.—The standard breeding cage.

milk, Bovril solution and honey solution, respectively, were suspended.* Each cage was stood on small glass blocks resting on two damp black filter papers in a petri dish (fig. 1). The experiment was carried out with seven cages arranged on a bench in a bay window facing south-east. Egg counts were begun from midday. The cages were moved every hour on to alternative petri dishes containing freshly damped filter papers, and a moist paint brush was used to remove any eggs still adhering to the nylon mesh on the bottom of the cage. During the hours of darkness a small inspection lamp was used in this process. The petri dishes containing the eggs of the previous hour were then removed so that the eggs could be counted with the minimum of disturbance to the flies. In this way, hourly egg counts were obtained throughout three separate periods of 24 hours. Throughout the observations a temperature record was kept, but no correlation with egg-laying was found.

Results.

Daily oviposition rhythm.

The hourly egg counts, the curves from two of which appear in fig. 2,A, clearly showed the presence of a daily egg-laying rhythm. Very few or no eggs were laid between midnight and midday and thereafter the number steadily rose to reach

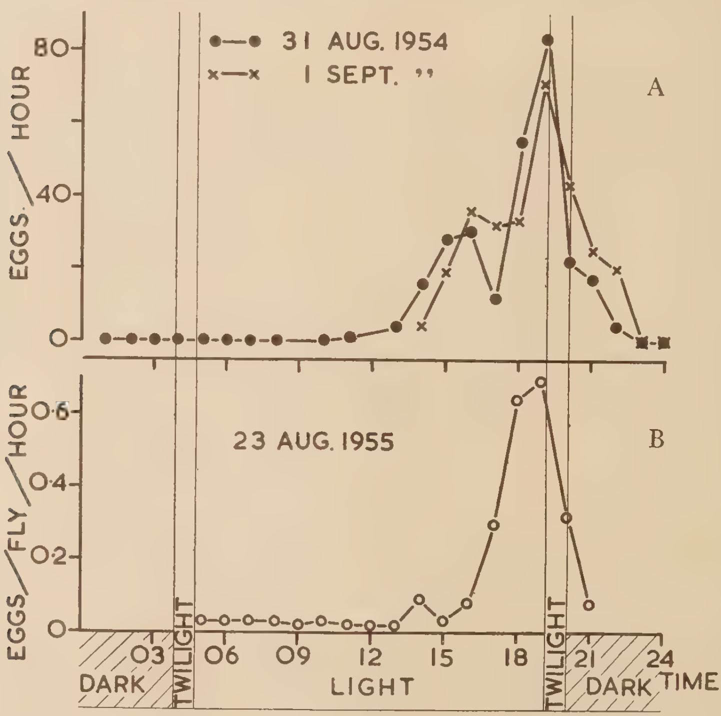

Fig. 2.—The daily oviposition rhythm.

a peak in the two hours before sunset, subsequently falling off rapidly to zero by midnight. This experiment was repeated in 1955 on a much larger scale, using 460 females in 46 cages, hourly observations being made from dawn (0500 hr.

* A more complete study of rearing techniques is given by Bardner & Kenten (1957).

G.M.T.) till dark (2100 hr. G.M.T.) over the period 22nd–24th August. Very similar results were obtained, with the times of peak of egg-laying coinciding (fig. 2,B).

The existence of this marked rhythm raises the question of the factors responsible for its initiation. To approach this problem, an experiment was set up in 1954 in which egg counts were taken throughout a 3-day period. On the first day the flies were kept in normal daylight until dark at 2100 hr. At this point the cages were transferred to a dark room and kept in conditions of continuous darkness until night fell in the evening of the second day at 2100 hr. The cages were then continuously illuminated with a "daylight lamp" which emitted both ultra-violet and visible light wavelengths. The results, which are given in fig. 3,

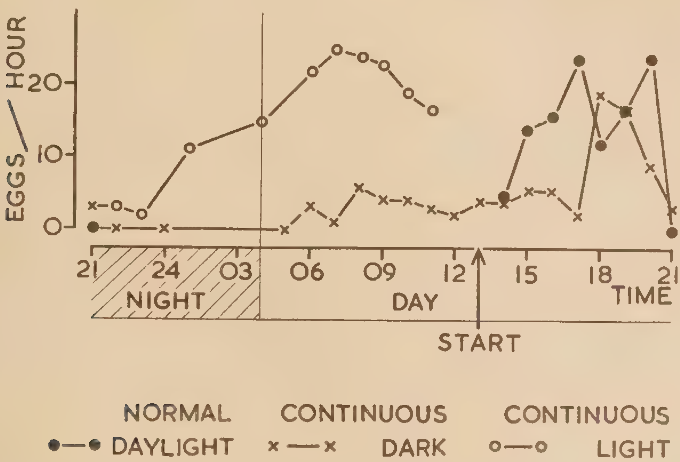

Fig. 3.—The effect of darkness and light on oviposition. Observations began at 1300 hr., at the point marked "Start", in normal daylight till 2100 hr.; this was followed by a 24-hr. period of continuous darkness, after which the cages were subjected to continuous light.

show that even in the absence of light the daily egg-laying rhythm, with the peak of laying in the two hours before sunset, can be maintained, at least for the first 24 hours. The results also suggest that exposure to continuous light may influence the rhythm and increase the rate of egg-laying, although from this experiment it was not clear whether the egg-laying peak early on the third day was attributable to the continuous light because the possibility could not be excluded that it was a delayed effect of the previous period of continuous darkness. Furthermore, it had to be discovered how long this period of increased egg-laying would last. Accordingly, on 24th August 1955, an experiment was set up in which controls were kept in normal daylight. Both experimental and control cages were exposed to normal daylight on 24th, and the oviposition curve in fig. 4,A is that for both sets of cages under these conditions. On 25th August the control cages were again exposed to normal daylight, whilst the experimental cages were kept in continuous darkness during the 24-hour period up to nightfall on 25th August. The egg-laying rhythm of the flies in the experimental cages whilst in the dark agreed very closely with that of the daylight controls (fig. 4,B). At nightfall on 25th August both sets of cages were exposed to continuous light, as were the cages in 1954. In the first 24-hour period under conditions of continuous light (fig. 4,C) both the experimental flies and those of the daylight control produced an early-morning peak, as observed in 1954, from which it may be concluded that

the light itself was responsible. The continuous darkness, to which the experimental cages had been subjected in the previous 24 hours, did, however, affect the times of egg-laying in these cages in this period. Thus flies which had been in normal daylight on the previous day had laid 80 per cent. by 0500 hr., whereas

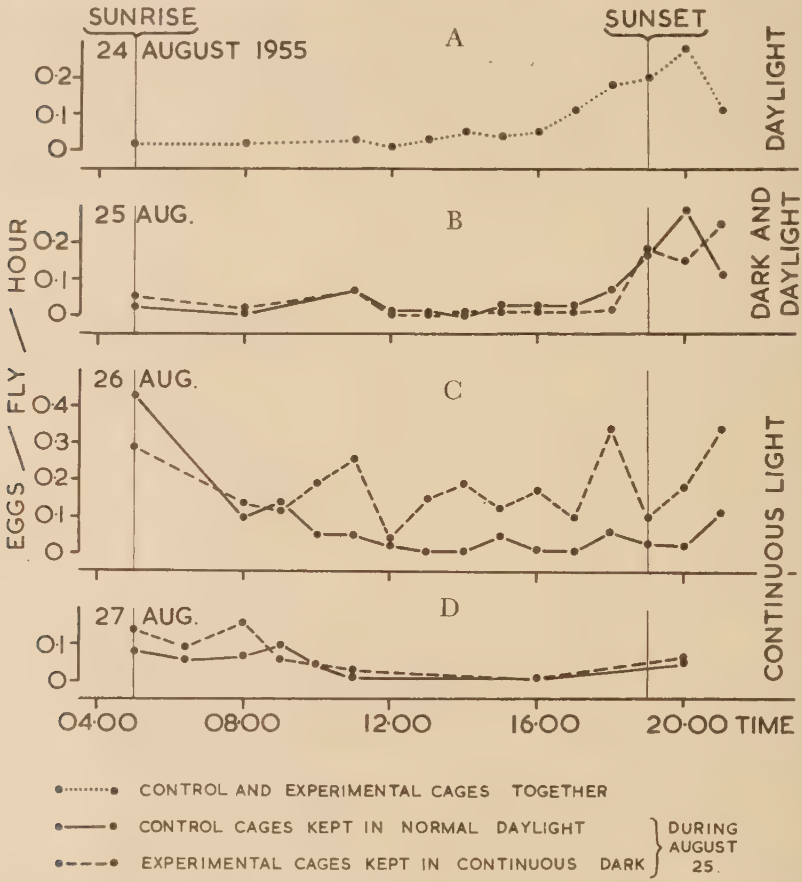

Fig. 4.—The effect of continuous light on the daily oviposition rhythm. A, normal rhythm; B, one set of cages in normal daylight, the other in continuous darkness; C, D, both sets of cages from B subjected to continuous light.

those which had been kept in darkness on the previous day had laid less than 40 per cent. by this time and their subsequent laying was much more erratic. It can also be seen from fig. 4, D that throughout the following day the normal rhythm (fig. 4, A) did not reappear in either set of cages but was replaced to a diminished extent by increased egg-laying in the early morning. By the fourth day of continuous light this new rhythm had virtually died away and was replaced by a low but fairly constant rate throughout the 24 hours. Although it may appear superficially that egg-laying follows as a consequence of exposure to light for a certain length of time this cannot be the simple operative factor as egg-laying occurs in the dark and a new daily rhythm may appear in continuous light.

As previously stated, it had been observed in 1954 that the rate of oviposition increased on changing the conditions from continuous darkness to continuous light. In 1955, a closer study of this effect showed that under conditions of

continuous darkness for a period of 24 hours the rate did not differ significantly from that of the control set of flies in normal daylight (fig. 5). Furthermore when both sets of flies were subsequently exposed to continuous light the numbers of eggs laid were similar, from which it appears that the rate was not influenced

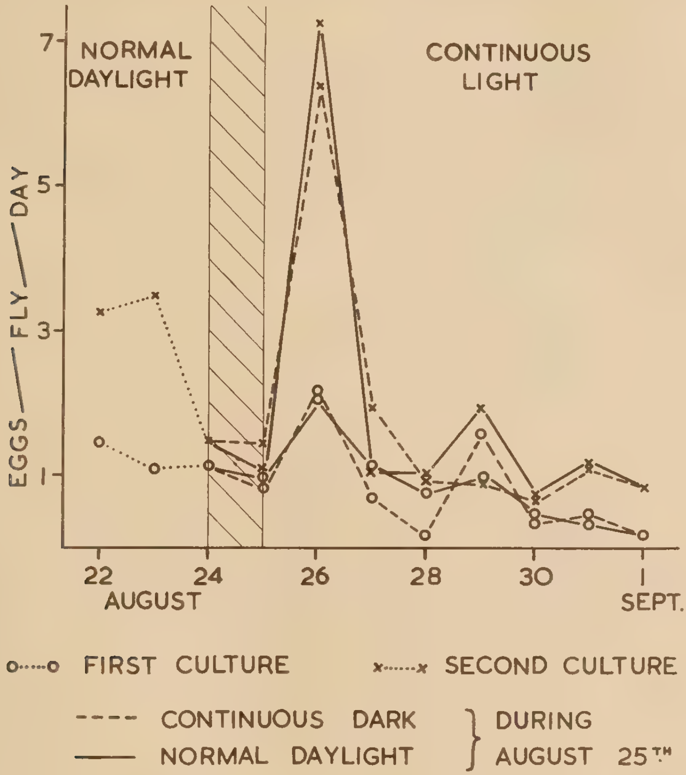

Fig. 5.—The effect of continuous light on the daily rate of oviposition of adults from two cultures of flies. Half of each batch was subjected to a 24-hr. period of continuous darkness immediately beforehand.

by a period of 24 hours' continuous darkness. On the other hand, as in the previous year, the continuous light does appear to have produced a marked though temporary increase after which there was a steady decline. This initial peak was not observed in 1956 when it was found from 16 experimental cages of 10 flies, with 16 cages of normal-daylight controls, that continuous light over a prolonged period did not significantly affect the overall laying rate.

In general, when in periods of continuous darkness, cultures experienced slightly higher and more uniform temperatures than when in normal daylight, but this did not appear to influence the egg-laying rhythm or the laying rate. As no rise in temperature was observed with continuous light, and the lamp was some distance from the cages, it seems most unlikely that temperature was involved in the temporary increase in the laying rate observed.

The egg-laying potential of the individual fly.

At weekly intervals from the first adult emergences, freshly caught flies were brought into the laboratory and individual pairs of male and female flies were set

up in breeding cages (fig. 1). Daily observations of the flies were made and the number of eggs laid recorded. Typical sets of results for three of the longest-lived flies are given in fig. 6.

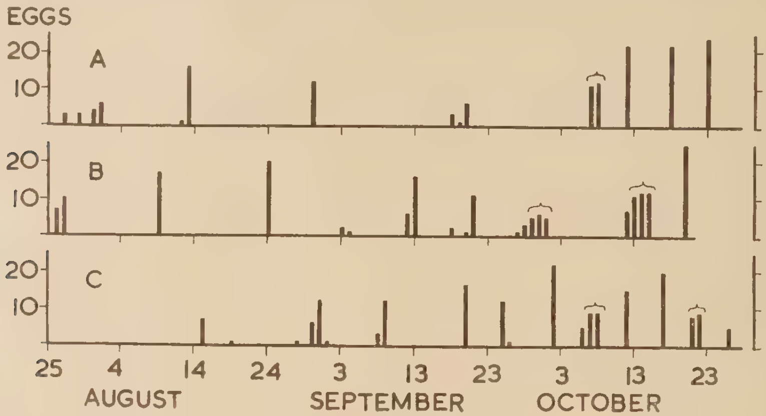

Fig. 6.—Periodicity in the individual oviposition of the three longest-lived flies. (Brackets indicate occasions when egg counts were not made at the usual time.)

From the results it could be seen that the fly tended to lay periodically in batches which may cover periods of one or more days. This periodicity was not observed in the experiments, already described (pp. 356–359), where each cage contained 20 freshly captured female flies, amongst which it was likely that there would be individuals in all stages of this oviposition cycle. An analysis of the numbers of eggs laid in each of these batches laid by single flies showed that the longer the period over which the batch is laid the lower the daily rate of laying (fig. 7). The decrease in rate, however, was not in proportion to the length of the period so that on average nearly three times as many eggs would be laid in a batch covering 6 days as in a batch laid in a single day. Furthermore, the mean

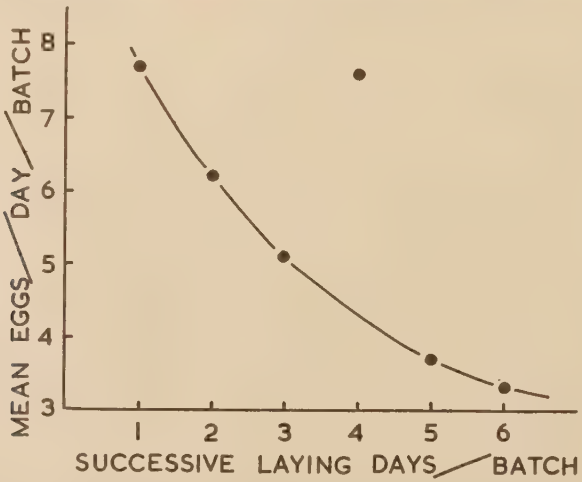

Fig. 7.—The number of successive days involved in laying one batch of eggs and the mean number of eggs laid per day for that batch.

numbers of eggs laid on each successive day of those occasions when laying took place over three or more consecutive days (fig. 8) suggests that there was a progressive increase in the rate of laying throughout the period. Whilst this was most marked for the three- and four-day periods, the mean number of eggs laid

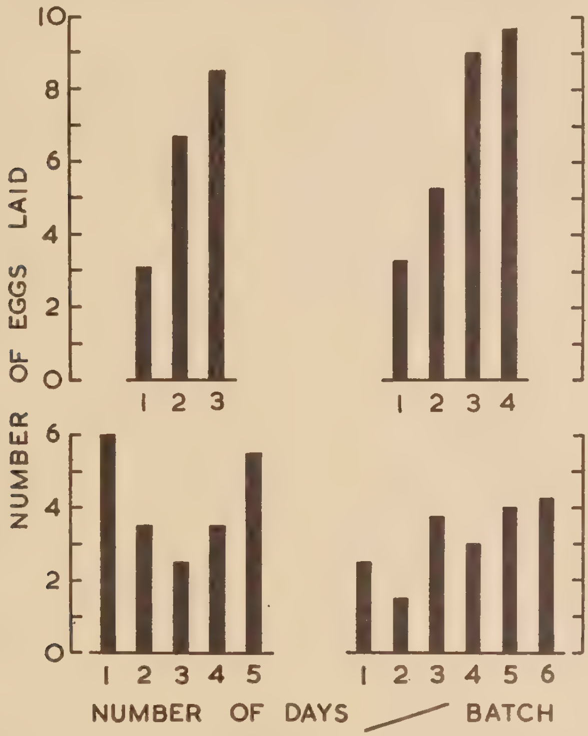

Fig. 8.—Mean numbers of eggs laid each successive day on those occasions when laying took place on three or more consecutive days.

on the last day of the six-day periods was nearly twice that laid on the first day of the series. Occasionally, in the intervals between the main batches, days occurred on which one or two isolated eggs would be laid. It is interesting to note that, in 1956, under the conditions of culture, 29 out of 40 flies or 73 per cent. came into laying and of these, five flies, or one-eighth of the total culture, laid more than a half of the 1,296 eggs obtained (Table I).

TABLE I.

Total numbers of eggs laid and the egg-laying period in days, in 29 cultures of isolated Wheat Bulb Fly.

Period	88	88	76	53	30	45	67	28	39	30	29	36	48	35	
Eggs laid ..	180	176	146	79	78	76	58	51	50	50	47	34	30	30	
Period	34	27	16	19	2	36	17	4	3	6	5	22	2	7	5
Eggs laid ..	26	24	21	19	19	17	15	12	12	10	10	8	8	7	3

Gough (1946) states each ovary has 16 ovarioles and I have also generally found this to be the case although up to 18 ovarioles have been counted on occasions. Gough also states that the eggs mature together, but this was not confirmed in observations based on frequent dissections made throughout the summer of 1956. A proportion of the eggs was generally found to be in advance of the remainder and it is interesting to note that the mean total for the first egg-laying was 12, the mean period between the first and second laying was 13 days and the mean total for the two was 26 eggs, so that even over this period the laying had not reached the full complement of 32 eggs. On those occasions when a laying took place on a day well separated from the previous and later layings the normal range was from 1 to 24 eggs and it can be seen in Table I that there is no clear relationship between the total number of eggs laid and the usual number of 32 ovarioles. This point is further illustrated in fig. 6; fly B, for example, laid only 3 eggs in the middle of one 3-week period, whilst between 12th–15th October it laid 42 eggs, 5 days later laid another 25 eggs and then died on 21st/22nd October with 24 matured eggs in its ovaries, making a total of 49 over the latter period of 2 to 3 days.

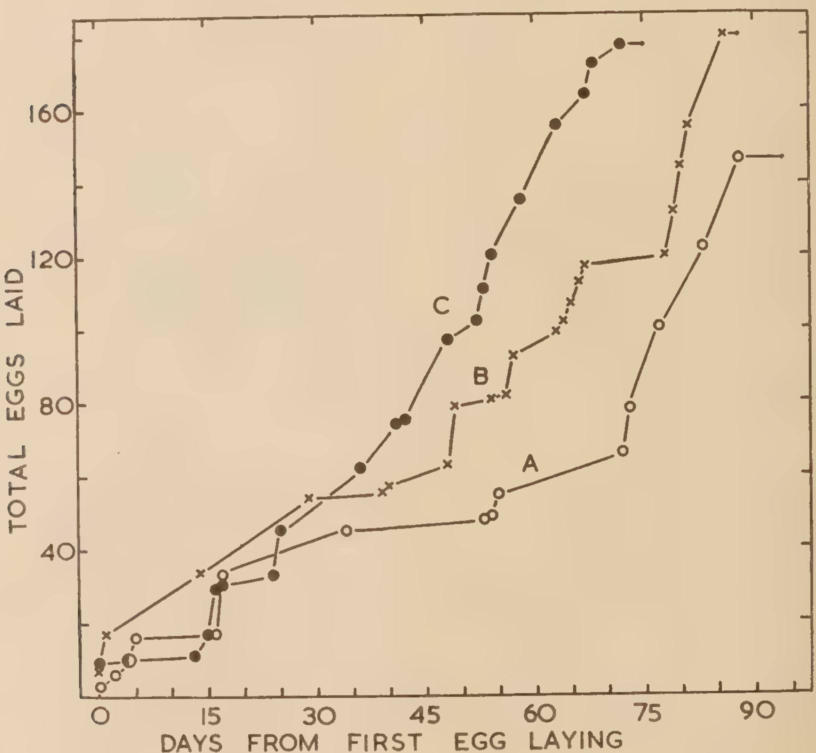

Fig. 9.—The increase in the rate of laying occurring with increasing age in the individual fly. The same data as in fig. 6.

The cumulative totals of eggs laid by the flies A, B and C in fig. 6 are shown in fig. 9. It can be seen that with increasing age the rate of egg-laying increases, largely due to a decrease in the periods between layings. The effect of this may

partly explain the curious grouping of the higher total numbers of eggs given in Table I. This effect may be responsible, in parallel cultures set up with 10 flies per cage, for the almost constant rate of egg-production throughout the experimental period in spite of the reduction in numbers of females by periodic deaths as shown in the examples in fig. 10.

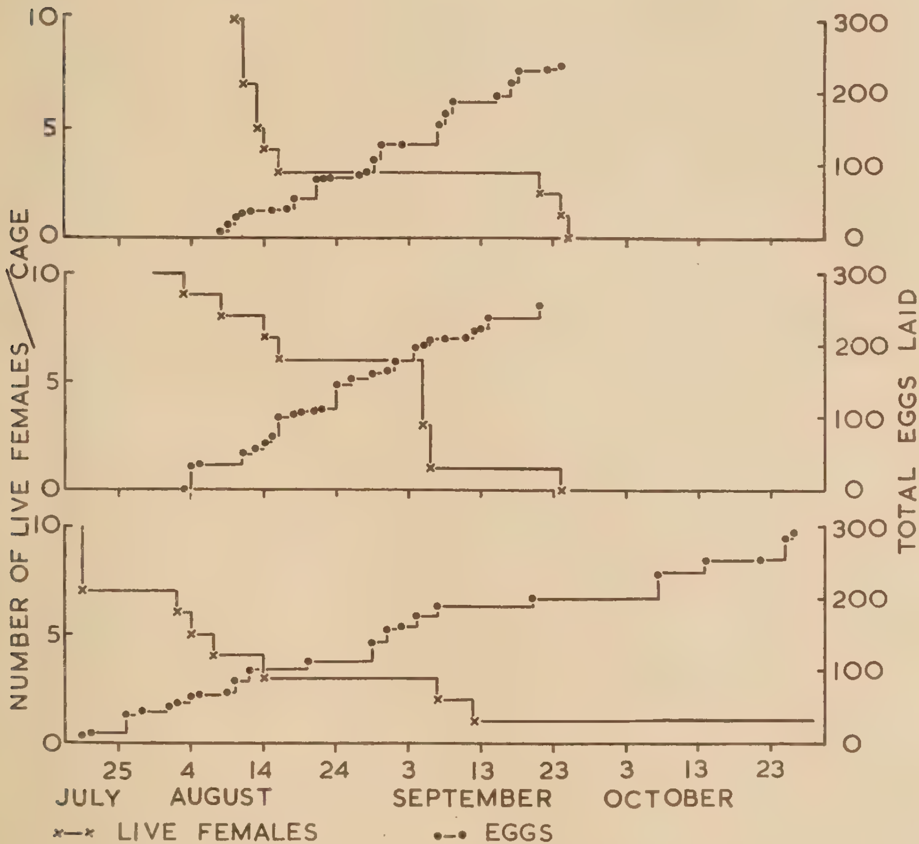

Fig. 10.—Egg-production in cages, initially containing 10 pairs of flies, in relation to the number of surviving females.

Discussion.

One of the noteworthy results of these observations in the laboratory was the low mean rate of egg-laying. The rate for the cultures of isolated flies given in Table I was 1·45 eggs/fly/day and that for parallel cultures of 10 flies per cage was 1·04, whilst similar rates were obtained in the course of other experiments. Judging from the longevity of many of the laboratory-reared flies and the total numbers of eggs laid, when compared with flies in the field, the conditions of culture appear to have been relatively favourable. Thus it may be expected that egg-laying in the field may be at similar or even lower rates. Should this be so it is not difficult to appreciate the failure to observe oviposition in the field and probably the best that may be expected would be the observation of Hedlund

reported by Rostrup (1924) where flies were seen to glide down over a fallow area and eggs were subsequently found in the soil.

This latter observation was made at 7 p.m., and Hedlund notes that egg-laying was only observed in the afternoons when the weather was clear and sunny and that, whatever the weather, egg-laying could not be observed in the mornings. These observations coincide well with the times of the oviposition rhythm, with maximum egg-laying in the evening, observed in the laboratory experiments. Why the flies should develop such a daily rhythm remains to be explained. The times and duration of daylight certainly appear to be factors, but, in view of the known periodicity of egg-laying, more information must be obtained about the factors leading to egg-laying before a complete interpretation can be made. Thus, flies which showed the continued rhythm of laying in darkness would most probably not have come from those which showed the rhythm in the previous few days, whilst those which showed the effect of light appear to have reacted to it immediately in that the tendencies built up from previous exposures to normal daylight were completely replaced. Amongst the crucial factors in these observations is that of the time of egg-maturation. An egg cannot be laid until it is fully developed, but the possibility always exists of egg-retention. Thus it is not clear from these experiments whether it is the rate of egg-development or the stimulus to lay already matured eggs that is associated with exposure to light.

It has been shown that the fly may in some of its periodical layings produce many more eggs than it has ovarioles. Dissections, however, have not given the impression that matured eggs are normally stored, so that it seems probable that eggs can be matured rapidly. Harlow (1956) found this with the blowfly, *Protophormia terrae-novae* (R.-D.), in which, unlike the Wheat Bulb Fly, all the eggs were in the same stage of development. The investigation of a possible effect of light on the rate of egg-maturation must await the results of later research.

It was shown (Long, 1958*a*) that adults of the Wheat Bulb Fly infesting a crop of wheat had a marked diurnal flight rhythm in which they tended to return to the crop in the afternoon and evening. This event would therefore coincide with the egg-laying rhythm. Whether the diurnal flight- and oviposition-rhythms are interrelated, or the former is also affected by light is at present unknown, but it might be expected that as a result of their interaction egg-laying would mostly take place in suitable sites near the infested crop as appears to have been the case (Long, 1958*b*).

With regard to the total number of eggs laid per fly, Rostrup (1924) quoting Hedlund suggests 20–40, whilst Gough (1946) considers that the first series of 32 eggs may be laid but questions the production of subsequent series. He obtained up to 50 eggs per female in the laboratory with an average of 22·5. Bardner & Kenten (1957) obtained up to 244 with an average of 29·9 also under laboratory conditions and on a diet of blood, condensed milk and honey. However, the egg-laying situation in the field cannot be deduced from these results although there is a small amount of evidence elsewhere to suggest that the mean laying rate may exceed 30 eggs per female. It was observed (Long, 1958*b*), that a survival of 10 per cent. was found between the egg and mid-larval stage so that from egg to fly may even be less. Brown (1955) states that 50 per cent. of eggs may survive as larvae, whilst Gough (1947) considered the survival to range between 20 and 50 per cent. in different areas, with a subsequent variable reduction of up to 70 per cent. within the larval stage itself. Dobson, Stephenson & Lofty (1958), using a large emergence cage, observed a survival of 5 per cent. from egg to fly, whilst noting that they obtained approximately equal numbers of males and females. They also estimated that within the cage about 20 per cent. of the females that emerged eventually came to maturity. From this it would follow that 0·5 per cent. of the total eggs laid would complete their development

as matured females the following summer and for a population to replace itself the females would each have to lay an average of 200 eggs. Although, as is carefully pointed out, conditions within the cage in this experiment may have influenced the results, and these estimates would tend to support this possibility, the mortality up to emergence would not have been affected. Assuming that the estimate of 20 per cent. for matured females was partly due to experimental conditions it would seem unlikely that maturation would occur in much over 50 per cent. of females in the field as only 73 per cent. (p. 361) was obtained under the relatively favourable conditions of laboratory rearing. Thus if a population is to replace itself with an average of 30 eggs per female it would be necessary for 3·3 per cent. of the eggs to develop into matured females and at least twice that number of female flies to have emerged. As populations may double in size from one year to the next (Long, 1958*b*) a conservative estimate for both males and females of a 25 per cent. survival from egg to adult, that would therefore be necessary, appears disproportionately large in relation to the former observations. These considerations would suggest that in the field about two per cent. of the eggs develop to mature females and the average number of eggs laid must frequently be nearer 50 per matured female.

How far the individual Wheat Bulb Fly may realise its egg-producing potential in the field largely depends on its nutritional state and this in turn will depend on a number of external factors. From unpublished work so far completed on this subject it appears that the nutritional requirements may be sufficiently exacting to prove a major limiting factor in the field.

Summary.

In laboratory cultures of Wheat Bulb Fly, *Leptohylemyia coarctata* (Fall.), a daily oviposition rhythm was observed in which egg-laying was virtually restricted to the afternoon and evening with maximum laying occurring in the two hours before nightfall. The time of oviposition coincided with that part of the diurnal flight rhythm, earlier observed, in which the flies actively congregated on wheat and this, it is suggested, could account for the fact, already recorded, that laying has been found to occur mostly on sites close to an infested crop.

The oviposition rhythm was maintained for 24 hours in absence of light and therefore appeared to be partly inherent. However, it could be influenced by the times of exposure to light and disappeared in constant light. Darkness did not appear to affect the egg-laying rate but a temporary increase followed exposure to continuous light. Within the course of the experiments the rate was not affected by small changes in temperature.

The individual fly laid up to 180 eggs in the laboratory in periodic batches of up to 42 eggs laid over periods of 1 to 6 days. This periodicity was obscured in cages containing a number of flies. Disproportionately small decreases in the mean daily laying rate occurred with increases in this laying period. Within the laying period the rate progressively increased with each successive day. The total number of eggs laid was not related to the number of ovarioles. In the laboratory, the rate of laying increased with age and most of the eggs were laid by relatively few flies.

The rate of egg-laying and survival at different stages in the field is discussed and it is suggested that about two per cent. of the eggs successfully develop as matured females which lay an average of about 50 eggs each.

Acknowledgements.

The author wishes to thank Dr. Marjory G. Morris for her help and advice in the statistical analysis of the periodicity in egg-laying. Thanks are also extended to Mrs. B. Copleston and Miss J. Balshaw for their assistance with routine breeding and to Dr. K. Mellanby for reading this manuscript.

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THE LEPIDOPTEROUS STALK BORERS ASSOCIATED WITH GRAMINEAE IN UGANDA.

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For many years agriculturists have felt the need for a full survey of the Lepidopterous stalk borers that attack cereals in Uganda. While it was well known that they caused serious damage to cereals in the adjoining territories of Kenya and Tanganyika, little was known of their pest status in this country.

The stalk borers recorded by Hargreaves (1940) from Uganda were *Busseola fusca* (Fuller), *Sesamia calamistis* Hmps., *S. cretica* (Led.) and *S. vuteria* (Stoll). Subsequently, Tams & Bowden (1953) recorded the following from Uganda: *Sesamia albivena* Hmps., *S. albivena sudanensis* Tams & Bowden, *S. oriaula* Tams & Bowden, *S. poebora* Tams & Bowden, *S. poephaga* Tams & Bowden and *Poenoma serrata* (Hmps.). The early records of *S. cretica* and *S. vuteria* have proved to be erroneous and the material concerned can be referred to *S. calamistis*.

Intensive collection during 1954–56 at Kawanda and at Serere, the two main research stations of the Department of Agriculture, Uganda (fig. 1, p. 376), has now yielded further species, and all the known ones are listed in Table I.

TABLE I.

Stalk borers known to occur in Uganda, 1956.

Noctuidae	Pyralidae
Busseola fusca (Fuller)	*Chilo zonellus* (Swinh.)
Busseola segeta Bowden	*Chilo* sp. n.
Sesamia albivena Hmps.	*Eldana saccharina* Wlk.
Sesamia albivena sudanensis Tams & Bowden	*Ematheudes* sp. n., near *helioderma* Meyr.
Sesamia botanephaga Tams & Bowden	*Ematheudes* sp.
Sesamia calamistis Hmps.	*Hypsotropa* sp. near *subcostella* Hmps.
Sesamia poebora Tams & Bowden	*Maliarpha separatella* Rag.
Sesamia poephaga Tams & Bowden	*Pectinigeria* sp. n.
Sesamia oriaula Tams & Bowden	Gen. et sp. n., near *Crambus*
Sesamia sp. n., near *cretica* (Led.)	
Poenoma serrata (Hmps.)	

Bionomics.

Laboratory studies have been made of the life-history of most of the important species and in due course it is hoped to be able to study the rarer ones. A full description of the various stages is beyond the scope of this paper but the important characters will be mentioned briefly under each species.

Wherever possible, life-history studies carried out in the laboratory have been confirmed or supplemented by field observations. The breeding techniques used in the laboratory were as follows. Freshly emerged pairs of each species were placed in large cages containing small transplanted host-plants (the host-plant used is mentioned in the text under the different species). After oviposition, the egg-masses were collected and placed in small tubes. On hatching, some larvae

were returned to the original breeding cage, a few more were put in further breeding cages and the remainder bred entirely in tubes. It was found by experience that a single small plant in a breeding cage could only support a very small number of larvae to maturity, but in order to observe the effect of a more normal attack the emergence from one entire egg-mass would be placed on one plant. When this plant was killed by the large number of larvae, they were removed and bred through in tubes. Ordinary 6 in. × 1 in. glass tubes were used, fitted with cloth-covered cotton-wool bungs. During the early larval stages, cuttings from young host-plants were used and it was found that these needed changing only every other day, when the larva was removed to a clean tube with fresh food. As a larva neared maturity it required older and thicker stems and these needed changing daily. In order to prevent the larva wandering about the tube after the change, it was introduced into a small tunnel bored into the end of the new stem. This continual handling of the larvae led to a slight increase in the length of life-cycle as compared with single larvae bred on single caged plants but this never amounted to more than a day or two, provided food was never allowed to run out.

Chilo zonellus (Swinh.).

A good description of the adults is given by Kapur (1950). He noted that amongst Indian specimens the males tended to be much smaller and darker than the females and this was found to be equally true of all those examined in Uganda.

The adults are short lived in the laboratory and even with food died within 60 hours. The pre-oviposition period is 24 hours and nearly all the eggs are laid the first night after emergence, the female then dying. However, some females will live a further night and lay a few more eggs before dying.

The eggs are laid in imbricated rows in groups of 50 to 100. The maximum laid by a female under observation was 417 in six groups. The eggs are almost translucent at first, turning opaque white on the first day and finally greyish when about to hatch. They are flattened, scale-like and ovoid. Groups of eggs are laid anywhere on the food-plant, though most frequently on the underside of the leaf near the midrib.

The incubation period in the laboratory was eight days and in most cases hatching takes place before daybreak. The young larva is positively phototropic and negatively geotropic and migrates to the top of the plant (maize or sorghum). Here it mines the sheath and often tunnels inside the midrib for several days. Subsequently it bores down inside the funnel of the plant or it may leave this and migrate down the stem, before entering it, just above an internode, and tunnelling upwards. In older plants of sorghum or maize, the whole larval life may be spent in the developing head or tassel, respectively. Frequently only one egg-mass will be found on a plant and only the funnel on that tiller will be mined, but later on all the tillers of that plant will be bored by nearly-mature larvae. Migration from tiller to tiller must therefore occur, and probably also from plant to plant.

The larval stage occupies from 28–33 days in the laboratory. During the final instar the larva prepares a pupal chamber. First it tunnels almost to the outside of the stem, leaving intact only a small disc of epidermal tissue, which dries out, becoming very conspicuous on the green stem. It then plugs the tunnel, about one inch below the exit disc, and pupates with the head upwards. The pupal chamber is a little different in a badly attacked head of sorghum or maize that has not emerged from the sheath; in this case the larva works its way to the outside of the rotting head and constructs a pupal chamber against the sheathing leaf. This chamber is about one inch long and half-an-inch wide and is made of frass and silken threads, with an exit disc cut into the leaf. The pre-pupal period is about 24 hours and emergence takes place eight to ten days later.

The life-cycle in the laboratory is thus about seven weeks (egg, 8 days; larva, 28–33; pre-pupa, 1; pupa, 8–10 days). Observations in the field indicate that under natural conditions the larval stages take only 15–20 days, thus giving a slightly shorter total life-cycle (32–39 days). There is no resting stage and under ideal conditions about 11 generations should occur in a year. It has been impossible to check by observations the actual number, as the breeding is not cyclic and all stages can be found at any one time. Development is probably slowed down in the dry season and mortality must then be high, since infestations at the beginning of the rains are less severe than later.

Busseola fusca (Fuller).

The most recent description of the adults is that given by Tams & Bowden (1953). Specimens in Uganda cover a wide range of colour forms, but these appear to bear no relation to altitude, locality, or time of emergence. In some, the forewing is reddish-brown under the typical pattern, while in others the forewing is fuscous all over, practically masking the pattern. The hind wing also varies, from white with straw-coloured veins to greyish-brown with fuscous veins.

The pre-oviposition period is 48 hours and laying takes place over three nights. The total life of the adult female is five nights or approximately 96 hours.

The eggs are laid in groups of about 70 at a time. A group consists of some 3–4 rows of eggs, each row being about half-an-inch long, with all the eggs closely adhering to one another. They are nearly always laid at the bottom of the stem, between the sheaths of the dying lower leaves and the stem itself. The egg is rounded, flattened at top and bottom, with finely fluted sides and is white when laid, gradually turning brownish as it develops. The maximum number laid by a caged female was 568, composed of 412 in six batches on the first night, 88 in one on the second, and 68 in one on the third, after which it died.

The egg hatches in 6–8 days and the young larva makes its way up the funnel of the plant (sorghum or maize), mining it in exactly the same way as does the larva of *C. zonellus*. As it matures, the larva migrates down the stem and then tunnels into it. The larval period in the laboratory was 45–50 days from hatching to pupation.

Although both tassels of maize and heads of sorghum are attacked by *B. fusca*, the maturing larva always tunnels into the stem, where pupation almost invariably takes place. The pupal chamber may be anything up to four in. long and the exit disc is considerably larger than that of *C. zonellus*. The larva can construct a crude cocoon of frass and silk and in the laboratory will very often do so. The pre-pupal period is about 24 hours and emergence from the pupa takes place after 14 days.

As the weather at Serere gets drier, in mid-November, the larvae of *B. fusca* enter a resting stage on reaching the final instar. No fresh frass is found, indicating that feeding has ceased, and no further pupae are formed. In a dry, dead stem, these larvae enter the resting stage wherever they happen to be; those in a living stem will emerge, migrate down to near ground level, re-enter the stem and tunnel below ground level before entering the resting stage. Such larvae show no further signs of activity until the end of the dry season and no pupae are formed until late March or early April.

Pole-Evans (1939) suggests that in South Africa the pupation of overwintering larvae is brought about by abundant rainfall. The beginning of the resting stage at Serere is always associated with a long, dry spell in November, and pupation does not take place until heavy and continuous rain has fallen over several days in late March or early April. Unfortunately, records are only available for two years, but the evidence strongly supports Pole-Evans' hypothesis.

During the rainy season, the full life-cycle of *B. fusca* is about 66 days (egg,

6–8; larva, 45–50; pre-pupa, 1; pupa, 14 days), but during the dry season it is about 200 days. There are 2–3 generations a year.

Busseola segeta Bowden.

This species was described by Bowden (1956) from material collected at Serere. The pre-oviposition period is 72 hours and laying takes place over three nights, the female life thus occupying six nights or approximately 120 hours. The male is much shorter lived and usually dies within 48 hours.

The eggs closely resemble those of *B. fusca* and are laid between the leaf sheath and the stem in groups of 30–100. The largest number laid by a female under observation was 309, of which 31 were laid on the first night, 273 on the second and five on the third.

The egg hatches after seven days and the larva bores straight into the stem of the host-plant (*Panicum maximum* or *Pennisetum purpureum*), usually just above a node. Until the larvae are about one-third grown they live gregariously; they then migrate to other stems and tunnel solitarily. The larval stage lasts 44–57 days in the laboratory.

Pupation occurs in the stem or in the leaf axils, where a crude cocoon is constructed; the stem is commonly used in *Pennisetum* and the leaf axil in *Panicum*. The pre-pupal period is 24 hours and the pupal period 10 days. No resting stage has been observed in the life-cycle in the field, where all stages can be found throughout the year.

Sesamia calamistis Hmps.

Tams & Bowden (1953) have re-described the adult. In specimens from Uganda, the forewing varies from light buff, with little fuscous irroration, through a darker buff, with more fuscous, to a distinctly pinkish form, heavily suffused with fuscous. This last form is easily confused with the dark form of *S. poephaga*. There is much variation in size, smaller specimens being commoner in finger millet (*Eleusine coracana*) and some of the grasses, and larger ones in maize and sorghum.

Under laboratory conditions, oviposition commences 24 hours after emergence and continues over 2–3 nights. The female will live for 72–96 hours but the male usually dies within 24 hours.

The eggs are very similar to those of *B. fusca*, both in size and general appearance, and are likewise laid between the leaf sheath and the stem, but the egg masses are very much smaller and rarely contain more than 20 eggs. The total number of eggs laid is about 300, the most recorded being 327.

The egg hatches in 7–9 days and the young larva usually bores straight into the stem, although the funnel is occasionally mined. In young plants, the larva burrows up and down to produce a typical "dead-heart". When about one-third grown, the larva migrates to another tiller or plant. On finger millet, the egg mass contains only about ten eggs, and the larvae will turn the whole stem into a maze of tunnels before migrating to other stems, each larva choosing a separate one; as many as six stems are needed to complete the life-cycle of a single larva. In finger millet, consequently, one invariably finds patches of plants with dead-hearts, all produced by the larvae from a single egg-mass. In older plants, particularly of maize or sorghum, the very small larvae seem unable to tunnel directly into the stem and instead eat their way round and round, eventually cutting right through it. Migration to other stems then usually occurs, though one or two larvae will often remain boring down into the still-living portion of the stem.

The larval stage takes 27–36 days in the laboratory. The pupal chamber of *S. calamistis* is not usually of the typical form with an exit disc. In finger millet, it is outside the stem, in the leaf axil, and consists of some living leaves

pulled together with silken threads, any crevices being sealed up with frass; in larger-stemmed plants, pupation occurs in either situation. The pre-pupal period is about 24 hours and the pupal period 10–12 days.

The life-cycle in the laboratory is about 45–58 days (egg, 7–9; larva, 27–36; pre-pupa, 1; pupa, 10–12 days). Breeding takes place all the year round, there being no resting stage, and it has been impossible to check the number of generations a year by observation in the field.

No detailed work has been done on the other species of *Sesamia* but a few brief notes are included below.

Sesamia poephaga Tams & Bowden.

This species is represented in Uganda by two very distinct colour forms. The typical form, as described by Tams & Bowden (1953), has a cartridge-buff forewing, measures 24–28 mm. in expanse and is not very common. The locally common form has a reddish-brown forewing and is considerably larger, measuring 32–35 mm. These forms seem to bear no relation to host-plant, time of emergence or locality.

Oviposition occurs between the leaf sheath and the stem and the larva enters the stem via the funnel, not directly, thus differing from *S. calamistis*. Pupation is nearly always in the stem and there is no resting stage.

Sesamia botanephaga Tams & Bowden.

Oviposition occurs between the leaf sheath and the stem and the larva enters the stem direct. Pupation is generally in the leaf axil and there is no resting stage.

Sesamia oriaula Tams & Bowden.

The biology appears to be very similar to that of *S. botanephaga*. Originally collected from the Ruwenzori range above 5,500 ft., it is now known to occur in swamps at Kawanda and Serere, and in the Bwamba valley.

Nothing is known of the life-history of the undescribed species of *Sesamia* that is recorded here, and *S. poebora*, *S. albivena* and *S. albivena sudanensis* are known only from the records in Tams & Bowden (1953); these authors also recorded *Poenoma serrata* from Uganda and mentioned that it pupates head downwards in the burrow.

Host-plants.

Every possible kind of host-plant in and around Serere has been examined at different times of the year. Both grasses and sedges are common host-plants and the only limiting factor seems to be that the stem must be thick enough to enable the larva to reach maturity. No plant has been given host-plant status until any larva found in it has been bred through to the adult stage. The host-plants known in Uganda up to the end of 1956 are given in Table II.

From Table II, a large number of species would appear to be of economic importance in that they attack cultivated plants. Fortunately this is not the case, as the only species that occur commonly in cultivated plants are *B. fusca*, *S. calamistis*, *S. poephaga* and *C. zonellus*. *Eldana saccharina* Wlk. only occurs in restricted areas (see p. 380), as is also the case with *Maliarpha separatella* Rag. *S. botanephaga* and *Pectinigeria* sp. are common in swamp plants and all the records from cultivated plants for these two species are from fields along swamp verges.

A large series of collections was made from wild host-plants during the rainy season, when cultivated crops were abundant. Isolated patches of grasses, far removed from any cultivation, were kept under observation during this period and it was found that small numbers of stalk borers were always present in them.

This answers the query of Jepson (1954, p. 25) who says " we should always ask ourselves whether high population density of a borer in a cultivated crop leads to attack on wild grasses in the immediate neighbourhood, or whether the borer is a normal member of the grass association ".

To find the effect on wild host-plants of a high population density in an adjacent cultivated crop, an experiment was laid down at Serere in 1955. Two different areas were used, one on high ground and the other on a seasonally swampy patch fairly close by. Both areas were in newly cultivated land and all the stalk borers that appeared in the experiments must have immigrated from the surrounding bush. On the high ground, small plots (10 × 7 yd.) of possible dry-land host-plants (see Table III) were planted in a large matrix of sorghum; in the swamp,

TABLE II.

Host-plants of stalk borers in Uganda.

Host-plant*	*Busseola fusca*	*Busseola segeta*	*Sesamia botanephaga*	*Sesamia calamistis*	*Sesamia oriaula*	*Sesamia poebora***	*Sesamia poephaga*	*Sesamia* sp. n., nr. *cretica*	*Chilo zonellus*	*Chilo* sp. n.	*Eldana saccharina*	*Ematheudes* sp. nr. *helioderma*	*Ematheudes* sp.	*Hypsotropa* sp. nr. *subcostella*	*Maliarpha separatella*	*Pectinigeria* sp. n.	Gen. et sp. n., nr. *Crambus*
ANDROPOGONEAE																	
Hyparrhenia rufa	x	x		x					x					x			
Rottboellia compressa		x	x	x			x		x			x					
Saccharum officinarum	x	x	x	x			x		x		x						
Sorghum vulgare	x	x	x	x			x		x		x	x					
S. verticilliflorum	x	x	x	x			x		x				x				
Vossia cuspidata	x	x	x	x	x		x		x	x				x		x	
ERAGROSTEAE																	
Eleusine coracana	x	x	x	x					x			x					
MAYDEAE																	
Zea mays	x	x	x	x			x		x		x					x	
ORYZEAE																	
Oryza sativa			x	x					x						x		
PANICEAE																	
Beckeropsis uniseta		x		x										x			
Echinochloa pyramidalis			x		x			x									
Panicum maximum	x	x		x			x	x	x					x			
Pennisetum purpureum	x	x	x	x	x	x	x	x	x							x	
Pennisetum typhoides	x								x								
Setaria splendida				x													
CYPERACEAE																	
Cyperus distans			x	x							x						
Cyperus papyrus			x								x						x
TYPHACEAE																	
Typha australis			x														

* The first five groups are sub-families of the Gramineae.
** Known only from the record in Tams & Bowden (1953).

similar plots of other possible host-plants were planted in a strip amongst the general swamp flora. Perennial grasses and sugar-cane were planted as sets, and the annual grasses and cereals were sown as seed. All the crop plants were weeded and well tended, but the grasses were left to grow wild.

Two series of borer-damage estimations were taken from these plots, one in August, when the cereals were harvested, and the other later, to see if any migration had occurred from the cereal trash into the wild hosts. Unfortunately, slashing the cereals after harvest was not a severe enough measure, as there was sufficient rainfall to enable the sorghum to tiller, and no migration took place beyond these sorghum tillers.

Samples consisted of 100 stems from each plot and 300 stems from the sorghum matrix, and the numbers of stems bored or not bored were counted. The numbers of larvae, pupae and cast pupal skins collected in this trial were small in relation to the numbers of bored stems, probably due to the drying mature stems being abandoned by the larvae. The numbers of immature stages of *C. zonellus*, *B. fusca* and *Sesamia* spp. (these last were not separately identified) are given in Table III and give some indication of the preferred host-plants of these species.

TABLE III.

Percentage of stems bored and the distribution of numbers of immature stages of *C. zonellus*, *B. fusca* and *Sesamia* spp. in various host-plants.

Host-plant	Stems bored (%)	*C. zonellus*	*B. fusca*	*Sesamia* spp.
Sorghum vulgare (matrix) ..	89	15	20	1
Pennisetum purpureum ..	50	5	11	0
Sorghum verticilliflorum ..	40	12	2	0
Saccharum officinarum ..	36	4	4	0
Zea mays	34	8	2	1
Panicum maximum ..	34	5	2	0
*Cyperus distans**	24	0	0	7
Pennisetum typhoides ..	20	1	4	0
*Oryza sativa**	16	0	0	8
Eleusine coracana	10	0	0	6
*Vossia cuspidata**	6	1	0	2
Hyparrhenia rufa	6	2	0	0
Echinochloa pyramidalis ..	0	0	0	0
Setaria sphacelata	0	0	0	0
Pennisetum polystachyon ..	0	0	0	0

* Swamp area; other host-plants from dry-land area.
All figures from the samples taken at harvest time (August).

The choice of host-plant under the conditions, particularly as indicated by the numbers of immature stages in *Pennisetum purpureum*, *Panicum maximum* and *S. verticilliflorum*, is especially interesting. These grasses are extremely common over most of the country and must always constitute a large reservoir of stalk borers near cultivation. Field observations during the cropping season strongly support the inference that can be drawn from these figures that, at Serere, *C. zonellus* is the commonest species, *B. fusca* the second commonest and species of *Sesamia* much less common.

Collections were also made from various host-plants during the dry season at Serere. This season is never absolutely dry but the rainfall is light and is spread over two or three days in each of the months of December to early March. Strong, dry winds blow most of the time and extensive burning is carried out

by the local peoples. Thus the vast numbers of stalk borers that are present at the beginning of the dry season are subsequently very severely reduced by the lack of suitable host-plants.

Accurate counts were made at the research station from mid-February to mid-March 1956. Table IV gives the numbers of larvae and pupae of the principal species collected from large numbers of stems of the more important hosts in this period.

TABLE IV.

Dry-season occurrence of the principal stalk borers at Serere, 1956.

Host-plant		*C. zonellus*		*B. fusca*		*Sesamia* spp.	
		Larvae	Pupae	Larvae	Pupae	Larvae	Pupae
Sorghum vulgare	—dry stems	132	74	12	0	3	5
,, ,,	—stubble	85	13	5	0	17	1
,, ,,	—living stems	417	69	13	0	104	15
Panicum maximum	— ,, ,,	5	0	0	0	9	3
Saccharum officinarum	— ,, ,,	4	1	3	0	0	0
Pennisetum purpureum	— ,, ,,	2	0	0	0	4	0
Sorghum verticilliflorum	— ,, ,,	15	2	0	0	6	0
Totals		660	159	33	0	143	24

During the dry season, *C. zonellus* is extremely common in sorghum trash and stubble and in the natural volunteer tillers. Breeding is evidently continuous, for fresh pupae were found daily over the whole dry season in one large field of slashed sorghum. Apparently *C. zonellus* makes little use of sugar-cane or wild host-plants to aid its survival during the dry season if sorghum is available.

Sesamia spp. (predominantly *S. calamistis* and *S. poephaga*) are also breeding actively at this time of year and their favourite hosts are volunteer sorghum, *S. verticilliflorum* and *P. maximum*. *B. fusca* is present only as a larva during the dry season and no pupae were found at all; even so, very few larvae were found and these were exclusively in cultivated crops.

One conclusion that is readily apparent from these observations is that the destruction of all forms of crop residue, except in areas where sorghum is deliberately ratooned over the dry season, would greatly reduce the numbers of borers carried over the dry season.

Survey and Distribution.

In this section it is proposed to give an outline of the importance and distribution in Uganda of the graminaceous crops and the more important wild host-plants of borers, together with a discussion of the damage caused by the latter in each plant, and finally the known distribution of the principal species of stalk borers.

Surveys of the Protectorate were commenced in late 1954 and continued intermittently in 1955 and 1956. In West Africa, Bowden and Sutherland (Jepson, 1954) sampled 100 stems from selected plots every twenty miles along a transect route. The surveys described here were more detailed, in that stops were made approximately every five miles. A random sample at each stop would obviously have been preferable, but difficulties were encountered and this could not be done. As a result, damage had to be estimated solely by eye, taking into account the number of dead-hearts, damaged funnels and entry or emergence holes seen in the plants. Any obviously damaged plants were cut open and the species of borer

present determined, either immediately or, where this was not possible, by rearing to the adult stage. The bulk of the survey work was done on the crops but nearby wild hosts were always examined wherever possible.

Rainfall plays an important part in the distribution of the crops and in the life-cycles of the various borers. Briefly, Uganda has two dry seasons, one at the beginning of the year and one at mid-year, the former becoming the more intense of the two as one goes northwards; the intervening periods are termed the first rains (January–June) and the second rains (July–December). The importance of the two rainy seasons differs in different parts of the country. This subject is fully dealt with by Manning (1956).

Distribution of host-plants and their susceptibility to attack by stalk borers.

Table V shows the total estimated acreage under cereals in each district of the Protectorate in 1955, with the individual crops given as percentages of this total. The administrative districts are shown in fig. 1.

TABLE V.

Distribution of different cereals in Uganda in 1955 *
(% of total cereal acreage in each district).

District	Total cereal acreage	Maize	Sorghum	Finger millet	Bulrush millet	Rice
Mengo	149,193	74·1	13·3	12·6	—	—
Masaka ..	14,581	38·6	55·3	6·1	—	—
Mubende ..	16,756	29·6	34·5	35·9	—	—
Lango	239,048	3·3	31·8	64·8	—	0·1
Acholi	155,184	1·4	26·3	71·1	1·2	—
West Nile ..	136,673	28·2	17·6	53·8	—	0·4
Karamoja ..	47,500	5·2	84·3	6·3	4·2	—
Busoga	232,050	39·4	0·59	60·0	—	0·01
Bukedi	224,690	8·4	6·2	85·3	—	0·1
Bugisu	126,184	25·8	8·6	65·6	—	—
Teso	435,754	1·4	29·0	68·6	0·7	0·3
Ankole	60,840	7·3	24·4	68·3	—	—
Bunyoro ..	25,594	27·3	4·6	68·1	—	—
Kigezi	241,744	11·2	67·5	21·3	—	—
Toro	54,901	36·3	8·7	50·3	—	4·7
Total and weighted means	2,140,511	17·7	24·8	56·9	0·3	0·3

* Compiled from Provincial Agricultural Officers' annual reports.

By far the most widely grown cereal in Uganda is sorghum (*Sorghum vulgare*); although the total acreage is well below that of finger millet, most peasants will have a plot, however small, of this crop. It is grown over an altitude range from 3,000–7,000 ft. above sea level by people of widely differing origins, each with their own preferred varieties. Nearly all of these tiller very heavily, particularly after an early attack by stalk borer or central-shoot fly (*Atherigona indica infuscata* Emd.), when widely spaced or when ratooned. In West Nile, Acholi, Lango and Teso, the varieties are distinct and usually grown separate from one another though they may be interplanted with other crops. In the rest of the country the tendency has been to select for a group of similar varieties and these are usually grown as a mixture.

In West Nile, Lango and central Acholi the crop is often ratooned over the January–February dry season. Ratooning occurs to a less extent around the

edges of Lake Victoria in Masaka, Mengo and Busoga, where the crop is sometimes ratooned over the June–July dry period. Two crops a year can be grown over most of the country except Karamoja, most areas concentrating on the crop following the main dry season with only occasional, scattered farms growing two crops a year.

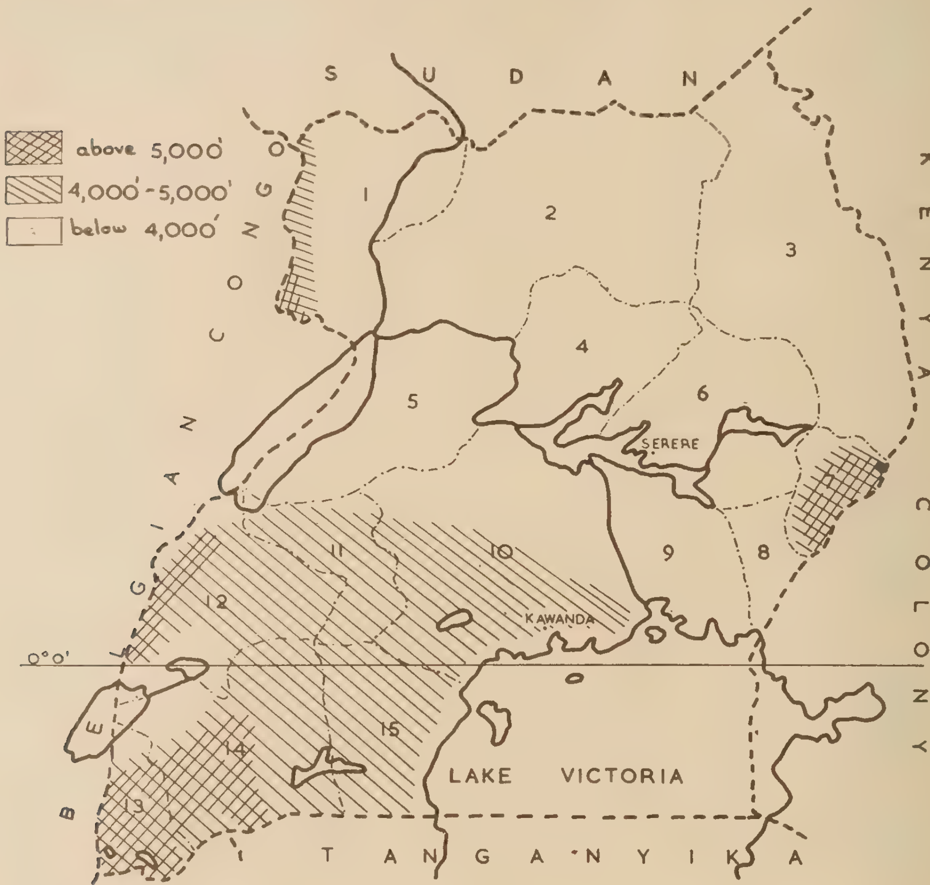

Fig. 1.—Map of Uganda showing physical features and districts.

Key:

1. West Nile	2. Acholi	3. Karamoja
4. Lango	5. Bunyoro	6. Teso
7. Bugisu	8. Bukedi	9. Busoga
10. Buganda	11. Mubende	12. Toro
13. Kigezi	14. Ankole	15. Masaka

In northern Uganda and Kigezi, sorghum is grown partially for food and partially for beer. Elsewhere it is used entirely for beer and, as it is only used as a "starter" for brewing banana beer, it is grown on a much smaller scale.

Sorghum is widely attacked by one or other of the major species of borer throughout the country. Typical damage is shown by "shot-holed" and tattered leaves and at its worst will prevent the seed head emerging. Experiments have shown that with as many as five larvae per stem, heavy yields can still be

obtained from big, thick-stemmed plants. It is usually very noticeable that spindly young tillers growing up amongst the older growth escape borer damage completely and although individually they will never yield as much as a thick stem that has been bored, collectively they can often out-yield a healthy single-stemmed plant.

Sorghum sown immediately after the main dry season, or ratoon sorghum developing at this time, is generally very lightly attacked. Second crops are more severely attacked, as they are exposed to a population of borers that has built up considerably, but excellent yields can be obtained.

Finger millet (*Eleusine coracana*) is grown over large areas, but not so widely as sorghum. It is the staple food of the peoples of northern and western Uganda, excepting the higher areas of Kigezi. In Acholi, Lango and Teso it may be dry sown in February, germinating with the so-called grass rains late in that month, or it may be sown when the main rains break in late March. In West Nile and Bunyoro it is grown in both first and second rains, in some areas it is planted in March–April and in others in July–August, but rarely in both rains in the same area. In east Mengo, Mubende, Toro, Ankole, Bugisu and the lower parts of Kigesi it is generally planted in August–September only.

Finger millet is rarely attacked by any borer other than *Sesamia calamistis*. Damage is limited to small patches of " dead-hearts ", caused by the larvae from one egg-mass, and is negligible in the crop.

Maize (*Zea mays*) is grown throughout the Protectorate, though only on a large scale in the districts bordering Lake Victoria (Mengo, Busoga and Masaka) and in the high ground of Bugisu, West Nile, Toro and Kigezi. In Mengo and Busoga it is grown as a cash crop and large quantities are exported from these two districts. In the rest of the country it is grown for home consumption or for sale in local markets. Around the Lake, the main crop is grown in the first rains while in the west it is grown in the second rains. In northern Uganda it is a very minor crop, grown only around the homestead; when sown in the first rains it gives a fair crop, but second-rains crops are very poor.

Maize is everywhere attacked by the commoner species of borer. Attack usually develops very late and frequently above the cob, *C. zonellus* being particularly common in the tassels. Cob-mining does occur but is more frequently caused by *Heliothis armigera* (Hb.) or *Argyroploce leucotreta* Meyr. than by the stalk borers. Coaker (1956) has shown that crops grown under adequate rainfall are apparently unaffected by borer damage.

Bulrush millet (*Pennisetum typhoides*) is a very minor crop in Uganda. It is very severely attacked by birds and consequently is grown only in the second rains, when the migratory weaver birds are less numerous. It is grown only in sandy soils in a few places in north Acholi, along the Sudan border, and a little in Karamoja and north Teso. The tough stem of bulrush millet appears to be particularly resistant to stalk borers and it is very rarely attacked.

Rice (*Oryza sativa*) is another very minor crop in Uganda. Highland rice is grown on some scale on the western side of the Ruwenzori range in Toro and a little in the north of West Nile. A small amount of swamp rice is grown in Lango, Teso and Bukedi. It is mainly a cash crop and might prove more popular with the peasant farmer if it were not so severely damaged by birds. It is mainly attacked by *Sesamia calamistis*, *S. botanephaga* and in Toro, west of the Ruwenzori range, by *Maliarpha separatella*.

Sugar-cane (*Saccharum officinarum*) is grown commercially only on two large estates near the source of the Nile. Elsewhere, tiny plots are cultivated around homesteads, in valley bottoms and along swamp verges. It is attacked by *Eldana saccharina* (West Nile only) and occasionally by *C. zonellus* and *S. calamistis*, but the damage is very slight.

Sorghum verticilliflorum, together with other wild species of *Sorghum*, is a

common weed of cultivated and waste land over most of Uganda. It is a common host of *C. zonellus*, *S. calamistis* and, to a lesser extent, *B. fusca*.

Pennisetum purpureum and *Panicum maximum* are very widely distributed grasses, occurring all over the country. All the principal species of borer are known to breed in them, but only *B. segeta* is common; fortunately this species is rare in cereal crops.

All the swamp plants (*Cyperus distans*, *C. papyrus*, *Vossia cuspidata* and *Echinochloa pyramidalis*) are hosts to a large number of species. At the present time they do not constitute a danger to cultivated crops but any large-scale clearing of swamps for rice or sugar-cane production would possibly lead to a heavy attack of stalk borers.

Distribution of the more common stalk borers.

Reference should be made to the maps given in figs. 1–3. In figs. 2 and 3, the heavy stippling indicates that the species concerned was numerous in plots examined in that area, while the light stippling indicates that it was rare but present in most plots examined. The two maps cannot be compared directly, as

Fig. 2.—Distribution of *Chilo zonellus* in Uganda. Key as for fig. 1. Density of stippling indicates the density of the species.

a "heavy" population of *C. zonellus* is numerically larger than a "heavy" population of *B. fusca*.

(*a*) *Chilo zonellus* (fig. 2). This species is widespread and common in Teso, Lango and Acholi, but in West Nile it disappears completely above 5,000 ft. It does not occur at all in Karamoja, except in a very restricted area in the Labwor Hills, on the Acholi border. It is common in north Bukedi and north Busoga, becoming noticeably less so in the south of these two districts; it does not occur in the mountainous district of Bugisu. It is rare in Bunyoro and north Mengo, becoming common in south Mengo and along the lake shore in Masaka. Practically all the rest of western Uganda is above 4,000 ft. (see fig. 1) and *C. zonellus* is not found at all. A single specimen is in the Kawanda collection from Busongora, on the southern slopes of the Ruwenzori range, but extensive searching in this area of Toro yielded no further specimens and this record must remain open to doubt.

It thus seems that *C. zonellus* cannot live much above 4,000 ft. in western Uganda or above 5,000 ft. in eastern or northern Uganda. Why there should be this 1,000-ft. difference between these two areas cannot be explained in terms

Fig. 3.—Distribution of *Busseola fusca* in Uganda. Key as for fig. 1. Density of stippling indicates the density of the species.

of rainfall, but temperature may be the limiting factor. Meteorological data is not available for Bugisu district or the south-western corner of West Nile, but comparison of the mean maximum and minimum temperatures of the high western area with those of the low northern area shows there to be a difference of approximately 10°F. the whole year round, the north being the hotter.

The complete lack of *C. zonellus* in Karamoja is probably due to the extreme conditions there in the dry season. The Karamojong are a nomadic tribe cultivating very few crops other than sorghum. The dominant grasses in the area are *Hyparrhenia* spp., *Setaria* spp. and *Themeda triandra*; the two latter are not known to be hosts, while *H. rufa* is rarely infested by *C. zonellus*. The dry season is severe, and grazing and burning remove practically all the grass in the district, leaving no host-plants to enable the species to carry over the dry season.

Although *C. zonellus* is not the most widely distributed borer in the country, it is the commonest. In dry years and in occasional out-of-season sowings it can do very severe damage. When, for instance, the rains have been very poor and the cereals are dwarfed and thin-stemmed, *C. zonellus* can cause total loss of the crop. Similarly, when one farmer sows a crop later than his neighbours, it will attract all the egg-laying adults from the surrounding more mature fields and heavy damage will result. Normal crops are rarely heavily attacked by this species and on the rare occasions that severe attacks have been found on such crops, yields have still been satisfactory. It seems highly likely that *C. zonellus* is a new introduction to Uganda, for earlier workers did not know it and there is no evidence that it was collected prior to about 1953. If it is a new introduction it might well adapt itself to local conditions still further and not only spread to the higher altitudes but become a far more important pest. At the moment, however, *C. zonellus* is rarely of economic importance in graminaceous crops in Uganda.

(*b*) *Busseola fusca* (fig. 3). This species is widely distributed throughout the country but is not as common as *C. zonellus*. In West Nile it is much commoner above 4,000 ft. than below, and in Lango and Acholi it is concentrated on the slightly higher ridge of land connecting the principal towns of Gulu and Lira. This ridge has a distinctly higher rainfall than the adjoining countryside and is much more intensively cultivated. In Karamoja, *B. fusca* is common in all the areas of cultivation. In Teso, Bugisu, Bukedi, Busoga and in the Lake areas of Mengo and Masaka it is extremely common. In western Uganda it is nowhere common except around the Ruwenzori range in Toro, and in Kigezi.

This seemingly rather erratic distribution closely fits the density of human population (Thomas & Scott, 1935, p. 272) and, consequently, the intensity of cultivation. *B. fusca*, although able to breed in many wild hosts, is apparently unable to exist in large numbers unless conditions suitable for the larval resting-stage occur. The wild grasses are severely burnt annually and this probably kills resting larvae, so that only those resting in crop trash and stubble in areas of cultivation can survive. Only in crops grown out of their normal season have severe attacks of *B. fusca* been found and, in general, it is not a major economic pest in Uganda.

(*c*) *Sesamia calamistis*. This pest is widely distributed throughout the country except in Karamoja, where it cannot survive the dry season. It is not very common and nowhere have any heavy attacks by it been recorded.

(*d*) *Sesamia poephaga*. This species has been bred from material collected from scattered points in the north and east of the country. It is probably more widely distributed than the records show to date but never of any importance.

(*e*) *Eldana saccharina*. This species is found fairly frequently in sorghum, maize and sugar-cane at scattered points along the Belgian Congo border. Except for the Lake Edward flats, where the species is not found, this is a high-altitude

belt, with relatively low temperatures and high rainfall. A few specimens have been collected from papyrus and sedge at Serere and Kawanda. It seems that as this species is unable to exist away from the higher altitudes except in swamps, high humidity might be the limiting factor. It is not a pest of any importance.

(*f*) *Maliarpha separatella.* This species has only been found attacking highland rice in Bwamba, west of Ruwenzori, where it is fairly common but not of any economic importance.

Parasites.

Parasitism in *S. calamistis* and the swamp-inhabiting species is high and may well be a limiting factor in keeping down their numbers; parasitism in the other species is low and probably exercises little control.

The commonest of all the parasites is a species of *Pediobius* (Eulophidae). Its hosts include *B. fusca*, *B. segeta*, *Sesamia* spp. and *C. zonellus.* The adult parasites emerge from the host pupa in large numbers, as many as a hundred having been recorded from a single pupa of *B. fusca.* It is most commonly found late in the year, from October to December.

Hyperchalcidia soudanensis Steffan (Chalcididae) is a fairly frequent parasite of *C. zonellus* early in the year, the adult parasite emerging from the host pupa. A Braconid, thought to be of the genus *Mesobracon*, has been commonly recorded from *Sesamia* larvae; the larva of this parasite emerges from the nearly mature host larva and pupates in a silken cocoon in the burrow, the adult parasite emerging nine days later. The Braconid, *Apanteles sesamiae* Cam., is the principal parasite of *S. calamistis* larvae and it has also been collected from *B. fusca* and *C. zonellus.* From ten to thirty parasite larvae emerge from a mature host larva and pupate together in silken cocoons in the host's burrow. An Ichneumonid belonging to a genus near *Chasmias* has been recorded from *Chilo zonellus*; the adult parasite emerges from the host pupa.

Two undetermined species of Phorid flies have been bred from pupae of *B. fusca*, the larvae emerging from the host and pupating in the frass in the burrow; a single pupa of the host will give rise to five or six individuals of one of these (*Diploneura* sp.) or as many as thirty of the other (*Plethysmochaeta* sp.).

Control.

Cultural methods which would probably help to reduce the stalk-borer attack in both sorghum and maize are as follows:—

(a) the destruction of all the trash, stubble and volunteer plants after harvest —this would not be possible in areas where sorghum is ratooned;

(b) the destruction, as far as possible, of all the representatives of wild species of *Sorghum* near to cultivation.

Indigenous parasites are probably one of the main factors controlling *Sesamia calamistis* in finger millet. *Busseola fusca* and *Chilo zonellus* are only lightly parasitised and it is probable that in their case the main controlling factors are climatic. As the stalk borers are rarely of any economic importance in cereals in Uganda, attempts to introduce exotic parasites would not be worthwhile.

Experiments on chemical control have been unsuccessful; it is hoped to describe these in a later paper. Many applications of insecticide are needed to control the continual attacks of *C. zonellus* and *Sesamia* spp. and this makes the control hopelessly uneconomic for the peasant farmer. No more than partial control was achieved in the trials, even with weekly applications of insecticide, and the treated plots yielded no more than the controls. These results on sorghum support the conclusions reached by Coaker (1956) working on maize in Buganda, and generally the two trials support the conclusion, reached in the survey, that stalk borers are not of major importance in Uganda.

Summary.

The Lepidopterous stalk borers that occur in Uganda in association with the Gramineae were studied there during 1954–1956 by collecting on all likely host-plants at two centres and by a country-wide survey in which stalk-borer damage in cereal crops was qualitatively assessed at five-mile intervals along the routes followed, and the species of borer present in such crops and, where possible, in nearby wild host-plants were determined. The commonest Noctuids were *Busseola fusca* (Fuller), *B. segeta* Bowden, *Sesamia calamistis* Hmps. and *S. poephaga* Tams & Bowden. All these attacked sorghum, maize, sugar-cane and (except the last) finger millet (*Eleusine coracana*); so also did *S. botanephaga* Tams & Bowden, but only near swamps, in which it infested sedges (*Cyperus* spp.) and reeds (*Typha australis*), from which the other species were virtually absent. Only *S. calamistis* and *S. botanephaga* attacked rice. All attacked *Pennisetum purpureum*, *Sorghum verticilliflorum*, *Vossia cuspidata* and (except *S. botanephaga*) *Panicum maximum*, and also other wild grasses.

B. fusca is widely distributed but most abundant in areas of intensive cultivation, where crop residues abound in which the resting larvae can survive the dry season. *B. segeta* is the most frequent species in *Pennisetum purpureum* and *Panicum maximum*, which are extremely common over most of the country, but is rare in cereal crops. *S. calamistis* (to which earlier records of *S. cretica* (Led.) and *S. vuteria* (Stoll) must be attributed) is not numerous but occurs in every district except Karamoja, where it cannot survive the dry season; and *S. poephaga* is known only from northern and eastern districts and is unimportant.

Chilo zonellus (Swinh.), which may be a recent introduction, occurs in all the cultivated host-plants and most of the wild ones except *Cyperus* and *Typha*; it has not been found at altitudes above 4,000 ft. in the west or 5,000 ft. in the north and east, but elsewhere it is the prevalent borer and can cause severe damage in dry years and on out-of-season crops. It was the only species besides *B. fusca* found on bulrush millet (*Pennisetum typhoides*), the tough stem of which resists attack. On the western border, *Eldana saccharina* Wlk. attacks sorghum, maize and sugar-cane at high altitudes, and *Maliarpha separatella* Rag. attacks rice. A fourth Pyralid, *Pectinigeria* sp., occurs on maize.

When small plots of host-plants were grown in a matrix of sorghum, and also in a swamp, and the whole sampled at harvest for borer infestation, all the cultivated hosts and many of the wild ones suffered some attack, the percentage of stems bored varying from 10 (finger millet) to 89 (sorghum) amongst the former, and reaching 34 (*Panicum maximum*), 40 (*Sorghum verticilliflorum*) and 50 (*Pennisetum purpureum*) amongst the latter. Immature stages of *C. zonellus* and *B. fusca* greatly outnumbered those of *Sesamia*, especially in the more heavily infested host-plants.

Notes are given on the life-histories of the commoner species of borer and on their habits in the field. In the laboratory, the lengths of the life-cycles, in days, were 68–75 (*B. fusca*), 65–78 (*B. segeta*), 46–58 (*S. calamistis*) and 46–53 (*C. zonellus*). In the dry season, the larvae of *B. fusca* entered a resting stage, which prolonged the life-cycle to 200 days; such larvae were found only in living or dry stems of crop plants. *C. zonellus* and *Sesamia* spp. bred continuously, in the dry season the former being found chiefly in trash, stubble and volunteer tillers of sorghum, the latter in these and living stems of grasses.

Of the principal cereal crops in Uganda, sorghum is the most widespread. The main crop, sown after the longer of the two dry seasons, suffers little borer attack; second crops are more severely affected, but plants with thick stems or numerous tillers nevertheless yield heavily. Finger millet is the staple food crop in the north and west; borer damage is negligible and restricted to small patches of "dead-hearts" caused by larvae from single egg-masses of *S. calamistis*. Maize is grown on a large scale in the districts bordering Lake Victoria and in the

highlands; borer attack is usually very late and, where rainfall is adequate, appears not to affect yields.

Apanteles sesamiae Cam. and another, unidentified, Braconid probably control *S. calamistis*, but on the other stalk borers the incidence of parasites, which are listed, is low. Destruction of all crop residues and wild species of *Sorghum* around cultivated areas would considerably reduce borer attack at the beginning of the growing season, but chemical control was only partly effective and did not increase the yield.

Acknowledgements.

I am very much indebted to Mr. A. P. G. Michelmore, Mr. P. E. S. Whalley and Mr. W. Hirst for advice and assistance; to my African staff for two years' extensive field collecting and work on the experiments; to the district Departmental staff for assistance in the surveys; to my colleagues at Serere for assistance in preparing the draft of this paper; to Dr. I. W. B. Nye and the staff of the Commonwealth Institute of Entomology for the identification of all the insects named; and to the Director of Agriculture, Uganda, with whose permission this paper is published.

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THE GROUNDNUT BRUCHID, *CARYEDON GONAGRA* (F.).

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Pest Infestation Laboratory, Slough, Bucks.

Groundnuts (the fruit of *Arachis hypogaea*, consisting of one, two or more kernels enclosed by a shell) are susceptible to damage by insects and fungi both before and after they have been harvested. Many insects that cannot penetrate the shell of the groundnut infest the kernels after shelling (Howe, 1952), but the Groundnut Bruchid is characterised by its habit of boring through the shell of the dried unshelled nut.

The Groundnut Bruchid is a troublesome pest in British and French West African territories. The extent of the damage it causes to the Gambian crop was shown by Hall (1954), who sampled unshelled nuts from twelve shipments to this country; in these, from 2·4 to 16 per cent. (mean, 5·5) of the nuts had been attacked, and a loss in weight of the order of 5–20 lb. per 200-lb. sack of nuts was recorded. The loss to the 1952–53 Gambian crop was estimated to be 3 per cent., or some 1,650 tons. In the Gambia, this beetle attacks unshelled nuts in storehouses (A. A. Green, unpublished). It can also breed quite successfully in shelled nuts stored either in warehouses or under laboratory conditions and it is occasionally found in bags of imported shelled nuts. Although Cotterell (1952) mentions it as occurring in nuts for export stored in bags in port transit stores at Lagos, it is not a serious pest of shelled groundnuts in Nigeria. It is thought that the weave of bags is sufficient to protect the shelled nuts from external infestation and that any infestation inside the bag originates from pre-adult stages present in the nuts previous to bagging or even to shelling.

In view of the economic importance of the Groundnut Bruchid, especially in the Gambia and Senegal, and the lack of detailed information on its control by insecticides, it was necessary to start laboratory experiments to obtain information on which insecticidal field trials could be based. As a preliminary, the optimum conditions for culturing the insect were investigated and a summary of the published information on its life-history, behaviour, distribution and host-plants was prepared. Some unpublished documents were also consulted. The results are presented in this paper, which aims to clarify the available information.

Taxonomy of Bruchid Beetles infesting Groundnuts.

Much confusion has existed in the past about the correct name for the Groundnut Bruchid. Bridwell (1929) recognised *Caryedon*, *Caryoborus* and *Pachymerus* as distinct genera, but differing views regarding their scope, and numerous misidentifications at the species level, notably as regards *acaciae* Gylh., *cassiae* Gylh., *fuscus* Goeze, *gonagra* F. and *longus* Pic, all of which appear to be distinct species, now placed in the genus *Caryedon*, have led to the appearance in the economic literature of many combinations of generic and specific names applied to this insect. The situation has recently been clarified by Southgate & Pope (1958), who have shown that the species of Bruchid commonly found on groundnuts is not *Caryedon fuscus* (Goeze), but *C. gonagra* (F.), to which all, or almost all, of the reports of the Groundnut Seed Beetle, or Groundnut Bruchid, should refer.

Minor confusion has been caused by Zacher (1951), who incorrectly attributed *C. fuscus* to Fabricius, and by the fact that Pic (1913), an author who has been widely followed, used the incorrect emendation *gonager* for *gonagra*. Furthermore, Pic identified as *Caryedon notativentris* Pic a number of specimens that are

at present in Zacher's collection. Some of these, and also certain specimens, thought to be wrongly identified, from other collections on which papers had been published, were obtained and examined by Mr. B. J. Southgate of this Laboratory and found to represent *C. gonagra*. These records are marked with an asterisk in Tables I, II and III.

TABLE I.

Records of Bruchids attacking groundnuts which are believed to refer to *C. gonagra*.

Name under which recorded	Author
Caryedon cassiae Gylh. ..	Decelle, 1951
C. fuscus Goeze	Bridwell, 1946 ; Cotterell, Howe, 1952 ; Hall, 1954 ; Zacher, 1954 (see Table III for other references)
Pachymerus acaciae Gylh.	Roubaud, 1916 ; Sagot & Bouffil, 1935 ; de Jonghe d'Ardoye, 1935 ; Vayssière, 1939 ; Hoffmann, 1945
P. cassiae Gylh.	Chevalier, 1936
P. chinensis L.	Roepke, 1917
P. longus Pic	Corby, 1941* ; Mackie, J. R., 1944 ; Beattie, 1946 ; Golding, 1946*

* These specimens have now been examined by Mr. B. J. Southgate and identified as *Caryedon gonagra* (F.).

Records of Bruchids attacking groundnuts are given in Table I, under the names given in the references cited. It is probable that all these records in fact represent *C. gonagra*, and that the records of other species are due to misidentifications. Material collected from groundnuts in French West Africa and sent to the Commonwealth Institute of Entomology in 1954 by Monsieur J. Appert as *Pachymerus cassiae*, the name applied to the Bruchid attacking groundnuts in that territory in place of *P. acaciae* (which was used formerly by Vayssière (1939) and others) has proved to be *C. gonagra*.

Food-plants of *Caryedon gonagra* **(F.).**

The only experimental work carried out recently on the food requirements of the Groundnut Bruchid is that by Prevett (1954), who found that it developed more rapidly in the pods of *Tamarindus indica* than in unshelled groundnuts, and that it did not breed at all in locust beans, cotton seed or cowpeas. Sagot & Bouffil (1935) investigated the life-history on tamarinds of what they termed *P. acaciae*, which was almost certainly *C. gonagra*. Zacher (1932, 1933) carried out some research into the development in seeds of *Cassia fistula* (1932) and pods of *Tamarindus indica* (1933) of what he termed *C. fuscus* in 1932 and *C. notativentris* in 1933; he also received living larvae of what he stated was the same species from India in *Acacia arabica*, but found that it did not breed in *Caesalpinia tinctoria* or *Albizzia lebbek*. This material has now been examined by Mr. B. J. Southgate and found to be *C. gonagra*.

Although, as a result of the work by Prevett (*op. cit.*), tamarind is thought to be the primary host-plant of *C. gonagra*, which has been recorded from it in many parts of the world, the latter is a major pest of groundnuts in the areas in which it has been collected from the stored product, that is, in Senegal (under the names of *P. acaciae* or *P. cassiae*), in Nigeria and Ghana (as *P. longus*) and in the Gambia (as *C. fuscus*).

A list of records of Bruchids attacking groundnuts, all of which are believed to represent *C. gonagra* under other names, is given in Table I. Records of attacks believed to be by this species, on the produce of plants other than *Arachis hypogaea* are given in Table II; it is interesting to note that, with one exception, all the host-plants recorded there belong to the Leguminosae. In Table III is given information summarised from numerous publications by Zacher, and from records of the United States Department of Agriculture, which is all believed to refer, in fact, to *C. gonagra*.

TABLE II.

Records of Bruchid attack on the produce of plants other than *Arachis hypogaea*, believed to refer to *C. gonagra*.

Host-plan recorded	Species name recorded*	Reference
Acacia sp.	—	Fletcher, 1914 ; Blair, 1935
A. arabica	*fuscus* Goeze	Mukerji & Chatterjee, 1951 ; Howe, 1952
A. farnesiana ..	—	Bridwell, 1918, 1919 ; Ghosh, 1925 ; Lever, 1942
A. pinnata	—	Mukerji & Chatterjee, 1951
Albizzia lebbek ..	—	Herford, 1935 ; Mukerji & Chatterjee, 1951
Bauhinia malabarica ..	—	Beeson, 1919 ; Blair, 1935
B. monandra ..	—	Bridwell, 1918 ; Greenwood, 1940 ; Lever, 1942
B. racemosa ..	—	Stebbing, 1914† ; Beeson, 1919 ; Reh, 1928 ; Blair, 1935 ; Mukerji & Chatterjee, 1951
B. tomentosa ..	—	Bridwell, 1918
Caesalpinia pulcherrima	—	Bridwell, 1918
Cassia sp.	—	Fletcher, 1914
,, ,, ...	*fuscus* Goeze	Herford, 1935
C. auriculata ..	—	Beeson, 1919
C. fistula	—	Cotes, 1893 (quoting Elditt, 1860) ; Stebbing, 1914 ; Bridwell, 1918 ; Beeson, 1919 ; Harada, 1940
C. grandis	—	Bridwell, 1918
C. montana	—	Beeson, 1919 ; Mukerji & Chatterjee, 1951
C. muritura	—	Stebbing, 1914
C. nodosa	—	Bridwell, 1918, 1919
Casuarina equisetifolia	—	Stebbing, 1914 ; Beeson, 1919
Colutea sp.	*fuscus* Goeze	Herford, 1935
Hardwickia binata ..	—	Beeson, 1919
Prosopis africana ..	*longus* Pic	Golding, 1946†
P. alba	—	Bridwell, 1920 ; Swezey, 1928
P. chilensis ..	*longus* Pic	Golding, 1946†
P. juliflora	—	Bridwell, 1918, 1919 ; Beeson, 1919
,, ,, ...	*longus* Pic	Golding, 1946†
P. oblonga	*longus* Pic	Corby, 1941
Tamarindus indica ..	—	Cotes, 1893 ; Maxwell-Lefroy, 1906, 1909 ; Fletcher, 1914 ; Stebbing, 1914† ; Bridwell, 1918 ; Ritchie, 1918† ; Beeson, 1919 ; Bridwell, 1920 ; Strong, 1922 ; Ghosh, 1925 ; Dammerman, 1929 ; Blair, 1935 ; Sohi, 1940 ; Lever, 1942, 1947 ; Mukerji & Chatterjee, 1951
,, ,, ..	*acaciae* Gylh.	Sagot & Bouffil, 1935
,, ,, ..	*fuscus* Goeze	Prevett, 1953†
,, ,, ..	*longus* Pic	Corby, 1941† ; Golding, 1946†

All the genera of host-plants listed above belong to the Leguminosae, except *Casuarina* (Casuarinaceae).

* Except where stated to be otherwise, the species name recorded is *gonagra* F. (or *gonager* F.), which is indicated by a dash. The generic assignments given in the original references have been omitted.

† The specimens that are the subjects of these references have now been identified by Mr. B. J. Southgate as *Caryedon gonagra*.

TABLE

Host-plant records published between 1921 and 1954 by F. Zacher or the United

Host-plant as recorded		Names under which Zacher's			
		Caryedon acaciae	*Caryedon cassiae*	*Caryedon fuscus*	*Caryedon notativentris*
Acacia sp.	(S)	—	—	1954	1954
A. arabica	(Z)	—	—	1954	1932, 1933, 1936, 1952
A. confusa		—	—	1952	—
A. farnesiana ..		—	—	1952	1933
A. senegal		—	—	1952	—
Albizzia lebbek		—	—	1932*	—
Arachis hypogaea ..	(Z)	1952	1952	1952, 1954	1936
Bauhinia acuminata		—	—	1952	—
B. galpini	(S)	—	—	1952	—
B. malabarica ..		—	—	1952	—
B. monandra ..		—	—	1932, 1952	1933
B. racemosa		—	—	1951	1933
B. tomentosa		—	—	1932, 1952	1933
Caesalpinia praecox ..		—	—	1952	—
C. pulcherrima ..		—	—	1932	1933
Cassia sp.	(Z)	—	1952	1954	1952
C. acutifolia		—	—	—	—
C. brewsterii	(S)	—	—	1952	—
C. fistula	(S)	—	—	1932, 1952	1933, 1936
C. foetida		—	—	1932	—
C. grandis		—	—	1932, 1952	1933
C. javanica	(S)	—	—	1952	—
C. kotschyana ..		—	—	1952	—
C. muritura		—	—	—	1933
C. montana		—	—	—	1933
C. nodosa	(S)	—	—	1932	1933
Casuarina sp.		—	—	1954	—
Colutea sp.		—	—	1952	—
Dialium guineense ..		—	—	1952	—
Erythrina monosperma		—	—	1952	—
Poinciana regia ..		—	—	1952	—
Prosopis africana ..		—	—	—	—
P. chilensis		—	—	1952	—
P. juliflora	(S)	—	—	1932, 1952	1933
P. spicigera		—	—	1952	—
Rhamnus purshiana ..		—	—	1951, 1952	—
Tamarindus indica ..	(S)	—	—	1932, 1951, 1952, 1954	1933
Terminalia arjuna ..		—	—	1952	—

S.R.A. = U.S. Dep. Agric. (1926–45). Service and Regulatory Announcements.

* Subsequently, Zacher (1933) states that breeding does not occur on this host-plant.

** Bridwell (1938) states that breeding does not occur on this host-plant.

(S) Specimens in the Smithsonian Collection labelled as from this host-plant have been identified by Mr. B. J. Southgate as *Caryedon gonagra* (F.).

(Z) Specimens in Zacher's collection labelled as from this host-plant have been identified by Mr. B. J. Southgate as *Caryedon gonagra* (F.), including specimens bearing the date 1931, collected from seeds of *Acacia arabica* and labelled *Caryedon notativentris* Pic in Pic's handwriting.

Note: The names that Zacher used for what he termed the Tamarind Seed Beetle, and for related Bruchids, differed in his successive publications, and they are listed below in the form in which he gave them, with explanatory notes added:—

1921. *Pachymerus acaciae* Gyll. (=*Caryoborus pallidus* Ol.). Zacher applies this name to a Bruchid attacking groundnuts in West Africa.

1927. *Caryoborus gonagra* F. Zacher applies this name to a Bruchid attacking tamarind seeds in India.

III.

States Department of Agriculture and believed to refer to *Caryedon gonagra* (F.).

records are given					Records under *Caryedon fuscus* Goeze in S.R.A.
Caryedon pallidus	*Caryoborus gonagra*	*Pachymerus acaciae*	*Pachymerus cassiae*	*Pachymerus longus*	
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	1927	—	—	—	—
—	—	—	—	—	1937
—	—	—	—	—	—
1933	—	1921	1954	1952, 1954	—
—	—	—	—	—	—
—	—	—	—	—	1948
—	—	—	—	—	1930
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	1937
—	—	—	—	—	1945
—	—	—	—	—	—
—	1927	—	—	—	—
1933	—	—	—	—	—
—	—	—	—	—	1943
—	—	—	—	—	1932
—	—	—	—	—	—
—	—	—	—	—	1936
—	—	—	—	—	—
—	—	—	—	—	1931
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	1933
—	—	—	—	—	1928**
—	—	—	—	—	1926
—	—	—	—	1952, 1954	—
—	—	—	—	—	—
—	—	—	—	—	1940
—	—	—	—	—	1930
—	—	—	—	—	1937
—	1927	—	—	1952, 1954	1930
—	—	—	—	—	1937

1932. Tamarind seed beetle, *Caryedon fuscus* Goeze (*Caryoborus gonagra* F., *languidus* Gyll.). Zacher puts a footnote in the text stating that, according to Pic, the material concerned was not *Caryedon fuscus* Goeze, but *C. notativentris* Pic.

1933. Tamarind seed beetle, *Caryedon notativentris* Pic (*Caryoborus gonager* F.). Zacher appears to imply here that records of *Caryoborus gonager* F. are based on misidentifications of *Caryedon notativentris* Pic.

Caryedon pallidus Ol. (*acaciae* Gyll.). Zacher here reverses his 1921 usage; in subsequent papers (1952, 1954) he treats *pallidus* Ol. as distinct from *acaciae* Gyll. and restricted to senna (*Cassia acutifolia*). It seems probable that *C. gonagra* (F.) does not occur on *Cassia acutifolia*.

1951. *Caryedon fuscus* F. Zacher applies this name to a Bruchid attacking tamarind seeds in India.

1952. *Caryedon acaciae* Gyll., *C. cassiae* Gyll., *C. fuscus* F. (*gonagra* F.), *C. notativentris* Pic, *C. pallidus* Ol. and *P.* (?) *longus* Pic. Zacher here treats all these as distinct species.

1954. *Caryedon notativentris* Pic, *C. pallidus* Ol. and *C. fuscus* Goeze (*gonager* F., *languidus* Gyll.), Tamarind weevil. Zacher here treats these as distinct species.

TABLE IV.

Records of specimens of *C. gonagra* (F.) in collections, or published records believed to refer to this species, showing the distribution.

Author of record or collector of specimen	Date of publication or collection	Original identification or name quoted in record*	Place of origin	Recorded source	Location of specimen**
			1. AFRICA		
			Gambia		
de Jonghe d'Ardoye, E.	1935	P.a.	—	Groundnut	—
Gordon, J.	1948	C.f.	—	—	B.M.
			Ghana		
—	1939	P.l.	—	Groundnut	Southern Rhodesia Entomological Section, Dept. of Agriculture
			Kenya		
Mac-Innes, D.	1934	P.l.	—	—	Coryndon Museum, Nairobi
			Nigeria		
Golding, F. D.	1939	C.l.	—	—	B.M.
Corby, H. D. R.	1941	P.l.	—	Tamarind and groundnut	—
Mackie, J. R.	1944	P.l.	Eastern Region	Groundnut	—
Cotterell, G. S.	1952	C.f.	—	Groundnut	—
Basden, E. B.	1947	P.l.	—	Groundnut	P.I.L.
Prevett, P. F.	1954	C.f.	—	Tamarind seeds	P.I.L.
			Portuguese Guinea		
—	1951	C.a.	—	—	Germany (Zacher colln.)
			Senegal		
Roubaud, E.	1916	P.a.	—	Groundnut	—
Sagot, R., & Bouffil, F.	1934	P.a.	—	Groundnut	—
de Jonghe d'Ardoye, E.	1935	P.a.	—	Groundnut	—
Vayssière, P.	1939	P.a.	—	Groundnut	—
Lepesme, P.	1945	P.a.	—	Tamarind and groundnut	—
Hoffmann, A.	1945	P.a.	—	Groundnut	—
—	1949	P.a.	—	Groundnut	Germany (Zacher colln.)
Appert, J.	1954	—	Bambey	—	P.I.L.
			South Africa		
—	1933	P.l.	†Bathurst	Stored groundnuts	B.M.
			South-West Africa		
Justice, J. N.	1929	—	Grootfontein	—	B.M.

			Sudan		
Bedford, H. W.	1936	C.f.	Khartoum	Bred from stored *sunt* seeds (*Acacia arabica*)	B.M.
Hussein, A.	1940	C.f.	Wadi-Halfa	*Tamarindus indica*	B.M.
			2. MALAGASY		
			Madagascar		
Friederichs, S. G.	1916	—	—	—	Germany (Zool. Mus. Humboldt-Univ.)
			Rodriguez		
Snell, H. J. & Thomasset, H. P.	1918	P.g.	—	—	B.M.
			Seychelles		
Percy Sladen Trust Expedition	1913	P.g.	—	—	B.M.
Shilthers-Merlas	—	C.g.	—	—	Germany (Zool. Mus. Humboldt-Univ.)
			3. ASIA		
			Burma		
—	1902	—	Prome	—	B.M.
—	—	C.g.	Tharrawaddy	—	B.M. (Andrews Bequest)
Weld Downing, A. K.	1922	—	—	—	B.M. (Andrews Bequest)
Malaise, R.	1934	P.g.	Myitkyina	—	Stockholm (Malaise colln.)
Ghosh, C. C.	1925	C.g.	Mandalay	—	—
			Ceylon		
—	1902	C.g.	Peradeniya	—	B.M.
			India		
Stebbing, E. P.	1903	C.g.	Widespread	*Tamarindus indica*	B.M.
—	1905	—	—	—	B.M. (Fry colln.)
Dr. Jaykar	1905	—	Bombay	—	B.M.
Bryant, G. E.	1908	—	Poonah	—	B.M.
—	1911	—	Dehra Dun	*Bauhinia malabarica*	B.M.
—	1922	C.g.	Belgaum	—	B.M. (Andrews Bequest)
—	1930	—	Coorg	—	B.M.
Maxwell-Lefroy, H.	1906	C.g.	New Delhi	Tamarind	—
Fletcher, T. B.	1914	C.g.	South India	Tamarind	—
Zacher, F.	1954	C.f.	—	—	—
			Iraq		
Ahmed, D.	1956	—	Abu-Ghraiba	Light trap	Division of Entomology, Directorate-General of Agriculture
			Israel		
—	—	—	—	*Acacia spirocarpa*	Israel (Div. Plant Protection)

TABLE IV (Continued).

Author of record or collector of specimen	Date of publication or collection	Original identification or name quoted in record*	Place of origin	Recorded source	Location of specimen**
			Java		
Bowring, S.	—	—	—	—	B.M.
Zacher, F.	1919	C.g.	—	*Bauhinia*	Germany (Zacher colln.)
Roepke, W.	1917	P.ch.	—	Groundnut	—
			Jordan		
Lumsden, W. H. R. ..	1942	—	Ghor Kereime	—	B.M.
			Malay Archipelago		
Dammerman, K. W. ..	1929	B.C.g.	—	Tamarind	—
			Pakistan		
—	1934	P.a.	Sind	*Acacia arabica*	Germany (Zacher colln.)
			Siam		
H.R.H. Prince of Champon	1921	—	—	—	B.M.
			4. OCEANIA		
			Fiji		
—	1921	P.g.	Lautoka	—	B.M.
Veitch, R.	1920	P.g.	—	—	B.M.
Greenwood, W.	1940	—	—	—	—
Lever, R. J. A. W. ..	1942 & 1947	P.g.	—	Tamarind	—
			Hawaii		
—	1908	C.g.	Kaimuki	—	Germany (Zacher colln.)
Bridwell, J. C.	1920	C.g.	—	Tamarind	—
—	1922	C.g.	—	*Cassia nodosa*	U.S.N.M.
Swezey, O. H.	1928	P.g.	—	—	—
Harada, T.	1940	P.g.	—	—	—
			Honolulu		
—	1911	—	Imported to Aburi in Ghana	*Hymenaea courbaril*	B.M.
—	1931 & 1937	—	—	Tamarind	U.S.N.M.
—	1948–1949	—	—	*Cassia javanica*	U.S.N.M.
			Tahiti		
Zimmerman, E. C. ..	—	—	Blue Lagoon–Papeete	—	B.M.

			5. CARIBBEAN AND SOUTH AMERICA		
Bowring, S.	—	—	—	—	B.M.
			Barbados		
Bovell, J. R.	—	C.g.	—	—	B.M.
			Curaçuo		
Simmonds, F. J.	1954	—	—	Tamarind	B.M.
			Dutch Guiana		
Bridwell, J. C.	1946	C.f.	—	—	—
			Hispaniola		
Bridwell, J. C.	1946	C.f.	—	—	—
			Jamaica		
Ritchie, A. H. ..	1917	C.g.	Hope gardens	Tamarind pods	B.M.
Ritchie, A. H.	1918	P.g.	—	Tamarind	—
Blair, K. G.	1935	P.g.	—	Tamarind	—

B.M. British Museum (Natural History).
P.I.L. Pest Infestation Laboratory, Slough.
U.S.N.M. Smithsonian Institution, United States National Museum.

* Key to abbreviations:—

B.C.g. *Bruchus (Caryoborus) gonager*
C.f. *Caryedon fuscus*
C.g. *Caryoborus gonagra* or *gonager*
C.l. *Caryedon longus*
P.a. *Pachymerus acaciae*
P.c. *P. cassiae*
P.ch. *P. chinensis*
P.g. *P. gonagra* or *gonager*
P.l. *P. longus*

** All the specimens listed in this column have been examined by Mr. B. J. Southgate, who believes them to represent *Caryedon gonagra* (F.).

† Bathurst, S. Africa, is not located in a groundnut-growing area. This specimen, therefore, is likely to have been imported into this part of Africa.

Distribution of *Caryedon gonagra.*

The distribution of the Groundnut Bruchid given in Table IV is based on specimens of *C. gonagra* whose identity has been checked, or on records in the literature that are believed to refer to this species. The insect is supposed to have originated in Asia (Elditt, 1860; Stebbing, 1914; Strong, 1922; de Jonghe d'Ardoye, 1935); Blair (1935) says it is an Indian species that has been largely distributed by commerce.

In India, Pakistan, Burma and Ceylon there are records of this species as the Tamarind Beetle, under the name *P. gonagra* or *Caryoborus gonagra.* It is widespread in India, being reported as far north as Dehra Dun, in the Punjab, and it also occurs in southern India and in Ceylon. In Burma, there is a record as far north as Myitkyina, and it is known from Siam and Java. It has been collected from scattered islands in the Indian Ocean and the Pacific Ocean.

In Africa, *Caryedon gonagra* is to be found in the north-east, west and south-west, but not in the south-east or north. According to de Jonghe d'Ardoye (1935) it is not found in the Congo. The only record from South Africa (see Table IV) is a specimen in the British Museum collection labelled " Bathurst, South Africa—stored groundnuts ". Bathurst is not a groundnut-growing area and it seems possible that this specimen represents an importation into South Africa of infested material. It is possible that the spread of *C. gonagra* from Asia to north-east Africa took place along trade routes and that the species was then transported by caravans to West Africa.

It is stated by de Jonghe d'Ardoye (1935) that the Groundnut Bruchid " est très répandue en Grèce, en Italie, en Egypte . . ." but the context of his remarks suggests that he may be referring to its occurrence in groundnuts imported into those countries, and there is no evidence to show that it has become otherwise established.

C. gonagra is not endemic in the West Indies, but it has become established there, having been taken probably in slave ships from Africa (Ritchie, 1918) to Jamaica, Haiti and Barbados. It has also spread to the mainland of South America, having become established in Dutch Guiana. It has not been found in the Argentine (de Jonghe d'Ardoye, 1935) but Bridwell (1946) expects it to become established in the United States.

Life-history of *Caryedon gonagra.**

Length of life of adult, oviposition and development.

Adults of *C. gonagra* do not take solid food and live for only a few weeks. Under my experimental conditions, they lived without water for three weeks. This result is compared with those of other workers given in Table V. It is presumed that during adult life reserves accumulated during larval life are used up. Prevett (1953) found that the provision of drinking water increased the average life of the adults from three weeks to six or seven weeks.

Mating can take place a few hours after emergence but usually occurs after one to two days (Mackie, 1946).

The stage during the harvesting of groundnuts at which *C. gonagra* lays its eggs is not definitely known. There is some evidence to show that eggs are laid on freshly harvested nuts that are being sun-dried before being taken into store (Corby, 1941) and eggs have been found adhering to tamarind pods that were still hanging on the tree (Sagot & Bouffil, 1934). Prevett (1953) showed that, in the laboratory, eggs were laid at the same rate and in the same numbers in the light as in the dark.

Prevett (1954) observed that females lay eggs from one day after emergence.

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* The evidence quoted here from previous workers is believed to refer to *C. gonagra*, although in most cases the authors used some other name (see above, and Table I).

apparently indiscriminately on any substrate. Where groundnuts are available, the translucent white, oval eggs (approximately 1 mm. long and 0·5 mm. wide) are stuck to the depressions in the shell of the nut or on the smooth testa of the kernels that are without their shell.

Mackie (1946) found that the mean number of eggs laid per day at 70 per cent. relative humidity was about three (maximum, 12) at 27°C. and two at 25°C. The daily rate of egg-laying was also shown to fall slightly with increasing age. Prevett (1953) found that up to 26 eggs are laid per day, 7–11 being the usual.

TABLE V.

Length of life of adults.

Laboratory observations

Temp. (°C.)	R. H. (%)	Approximate length of life in weeks		Author
		Without water	With water	
25	60	$1\frac{1}{2}$ – 5	3 – 11	Prevett, 1953
27	70	3 – 5	—	Mackie, 1946
28	50	3 – 6	—	Mackie, 1946
30	70	3	—	Davey

Field observations

Nigeria	12–32 days	Corby, 1941
French West Africa ..	Up to 50 days	Sagot & Bouffil, 1934

Egg-laying continues for 6–15 days (Corby, 1941). The peak occurs 5–6 days after the beginning of oviposition but the effect of providing water for the adults is to increase the oviposition period from about 14 to over 28 days and the number of eggs laid from a mean of 32 (range 6–99) to 45 (range 15–93) (Prevett, 1953). Lepesme (1945) records the minimum total of eggs per female as 40, for what he terms *P. acaciae*.

Eggs hatch after 9–10 days at 25°C. (Prevett, 1953), 7 days at 27°C. (Mackie, 1946), 6–8 days at 28°C. (Zacher, 1933) or 8–10 days according to temperature (Lepesme, 1944). The incubation period is given as about 6 days in Nigeria (Corby, 1941), and as 8–15 by de Jonghe d'Ardoye (1935).

Many authors have described how, on hatching, the larva invariably cuts through its shell at the point where this adheres to the cortex of the nut and burrows through the latter into the kernel. The small hole in the shell of the nut can usually be seen with the aid of a lens, through the transparent egg-shell, although it is sometimes covered by a yellow, granular material. When the egg-shell shrivels or is knocked off, these holes are difficult to locate. There are no other external signs of the presence of a developing larva in the kernel of the nut.

The experiments described below showed that a larva does not leave a whole unshelled nut before it is fully grown. It then makes a hole 2–3 mm. in diameter through the shell. The papery-like pupal case is then formed within the shell of the nut, blocking or protruding from the hole, or the full-grown larva may leave the nut and pupate in a case stuck on to the outside. The mature larva is also able to travel some distance from the nut in which it developed before pupating. This was observed by R. W. Howe (private communication) in Kano, Nigeria, where he noticed hundreds of such larvae crawling

away from a stack of *Cassia* pods, awaiting use in tanning. The stack had heated considerably.

The first-generation adults hatch while the nuts are in store. Work carried out at this laboratory shows that the newly emerged adults are able to make their way to any part of a pile of stored unshelled nuts. Copulation, however, does not take place in the confined spaces between the nuts, but at the surface of the heap. Should there be no available space at the surface of the nuts, as in a full sack, in which the sacking restricts the movement of the adults, then copulation and hence infestation is minimised. Mated females can move relatively freely and lay eggs throughout a bulk of stored unshelled nuts, but they are apparently unable to move as freely between shelled nuts (Corby, 1941; Prevett, 1954).

Descriptions of egg-laying and development in seed pods of *Tamarindus indica* have been given by Maxwell-Lefroy (1909), Sohi (1940), Corby (1941) and Lever (1942), and in *Cassia fistula* by Elditt (1860).

The number of larvae which can develop in a single unshelled groundnut.

Twelve female * adults of *C. gonagra* were confined singly, each on an intact unshelled groundnut (Gambian) in a 3 in. × 1 in. glass tube at 30°C. and 70 per cent. relative humidity. A similar series, using ten female adults, was set up using kernels from which the shells had been removed.

The females were allowed to lay eggs for about a week, by which time from 10 to over 60 eggs had been deposited on each nut or kernel. After a further fortnight, a number of the eggs had hatched (4–34 on each nut, the exact number

TABLE VI.

Pre-adult developmental period of *C. gonagra* (in days).

Temp. (°C.)	Relative humidity (%)				Author
	50	60	70	90	
35	—	—	No development		Davey
30–35	—	—	56–84	—	de Jonghe d'Ardoye (1935)
32	55	—	56	Mould prevented development	Mackie (1946)
30	—	—	42	—	Davey
28	50	—	—	—	Zacher (1933)
27	72	—	69	—	Mackie (1946)
25	—	91–98	—	—	Prevett (1953)
25	—	—	91–98	—	Davey
24·5	—	72–88	—	—	Zacher (1933)
23	135	—	123	142	Mackie (1946)
Nigeria*	73				Corby (1941)
French West Africa*	approx. 50				Sagot & Bouffil (1934)

* Observations under ambient conditions.

not being easy to ascertain). The number of adults that finally emerged from the unshelled nuts was only a small proportion of the number of eggs laid; an average of 6·5 ± 2 emerged from each unshelled nut and 2·4 ± 1 from each shelled kernel. Since each unshelled nut contained two kernels it is evident that

* See Appendix for characters distinguishing male from female beetles.

from each unshelled kernel there was an average emergence of nearly one more adult than from a shelled one, thus indicating that conditions are more favourable for larval development in unshelled than in shelled nuts (see also p. 399).

The effect of temperature and humidity.

Records in the literature, believed to refer to *C. gonagra*, for the development period from egg to adult at different temperatures and humidities are given in Table VI. Mackie (1946) in his experiments used ten nuts (it is not clear from the abstract of his report whether the nuts were shelled or unshelled) on each of which one egg had been laid for each of three conditions; because of infertility of the eggs, only 35 per cent. developed to the adult stage. Prevett (1953) used one pair of adults on two unshelled nuts in a 2 in. × 1 in. glass tube. In my experiments, a larger quantity of nuts and more adults were used (see p. 396), at temperatures of 30° and 35°C. The developmental period at 25°C. was determined from stock insectary cultures and was between 91 and 98 days, which agrees well with Prevett's (1953) results.

Production of the maximum number of F_1 adults on different food media.

(*A*) *Shelled nuts*.—The following experiments were designed to find the number of parental adults that are required to produce the maximum first filial (F_1) generation from a given quantity of shelled nuts at the temperature (30°C.) and relative humidity (70 per cent.) at which development had been found to be most rapid (see Table VI).

It was calculated from the work of Mackie (1946) that in 21 days five pairs of adults would infest 300 kernels and ten pairs would produce overcrowding, providing each female laid an average of three viable eggs each day. It was found from experiments that there was, in fact, no overcrowding when ten pairs of adults were used.

A further experiment was carried out with 5, 10, 25 and 50 pairs of adults (Table VII, expt. 1). Only shelled nuts were used and tests were made separately

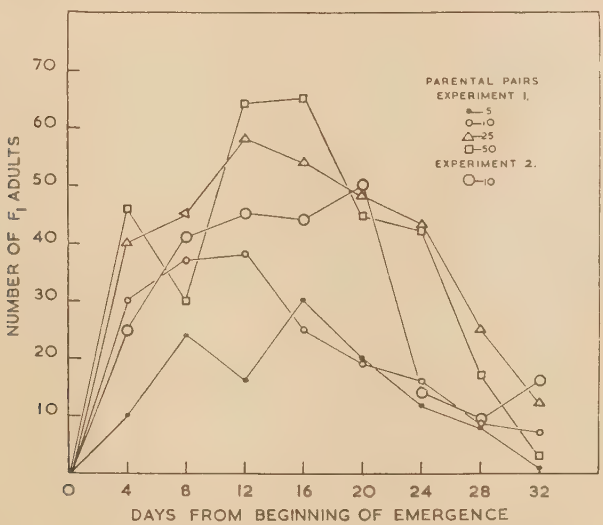

Fig. 1.—Numbers of F_1 adults of *C. gonagra* emerging in successive 4-day periods from cultures started with 5, 10, 25 or 50 pairs of adults (expt. 1) or 5♂♂ with 10♀♀ (expt. 2), using shelled groundnuts as food. Cultures kept at 30°C. and 70% R.H.

with a mixture, consisting of half, broken and intact kernels (expt. 1), and with hand-sorted intact kernels (expt. 2), 400 kernels weighing 160 g. In experiment 1, the parental adults, which were 0–10 days old at the outset of the experiment and thus near the peak of their egg-laying, were allowed to remain on the nuts for three weeks before being removed. Nearly all were then dead.

The first adults emerged six weeks after the start of egg-laying, and the average number of adults that emerged in subsequent consecutive four-day periods is shown in fig. 1. More beetles emerged from cultures started with 25 pairs of adults than from those with 10 pairs, but there appeared to be little further increase in the number of adults produced when cultures were started with 50 pairs of beetles.

TABLE VII.

Production of F_1 adults of *C. gonagra* on shelled groundnuts at 30°C. and 70 per cent. R.H.

Experiment	No. of pairs of parental adults	Age (days)	No. of replicates	Condition of kernels used	Weight of kernels at start (g.)	Total F_1 emergence per 100 g. kernels	Average F_1 emergence per 4-day period (1)
1	5	0–10	2	Mixed, broken	160	76	20
	10	0–10	2	,, ,,	160	113	25
	25	4	2	,, ,,	160	196	51
	50	5–10	2	,, ,,	160	200	54
2(a)	(2) 10♀♀ 5♂♂	0–4	1	Intact	150	161	} 38 (3)
(b)	10♀♀ 5♂♂	0–4	3	,,	150	170	

(1) These averages were calculated from the number of F_1 adults which emerged during the four 4-day emergence periods between days 8–24, fig. 1.
(2) Parental adults left on the nuts for 1 week only; in all the other cultures, they were left for 3 weeks.
(3) Results for (a) and (b) were similar and were therefore averaged for presentation in fig. 1.

Experiment 2 (Table VII) was set up using intact kernels, with 10 females and 5 males in each culture, in an attempt to produce both (a) a light infestation, by allowing the females to lay eggs for one week only, and (b) a heavy infestation, by allowing the adults to remain on the kernels for three weeks. Table VII shows that approximately the same number of F_1 adults emerged from both treatments (a) and (b), indicating that most of the egg-laying must occur during the first 11 days of adult life. The number of adults emerging in successive four-day periods, averaged for parts (a) and (b) of experiment 2, are shown in fig. 1.

In these experiments, a smaller number of adults was obtained from the cultures in which a mixture of broken and intact kernels was used than from cultures using the same number of females on intact kernels only. This may have been due to the presence of a higher proportion of males in the former experiment, which might have caused interference with egg-laying, or to an effect of the insects crowding on to the intact kernels available amongst the mixture, or to the presence of free fatty acids (F.F.A.) in the rather poorer-quality unsorted kernels.

(*B*) *Shelled nuts, unshelled nuts, and shelled nuts with coarsely ground shell added.*—A preliminary experiment indicated that more adults of *C. gonagra* emerged from unshelled nuts than from shelled ones. A comparison was therefore made of three different food media as regards the number of F_1 adults obtained from cultures on them.

Two replicates of each medium were set up, each consisting of a 2-lb. glass jar containing 160 g. food on which ten pairs of adults, aged 0–4 days, were left

for one week; the media used were Gambian nuts that were unshelled, shelled, and shelled but with 3 g. ground shell added per jar. They were kept at 30°C. and 70 per cent. relative humidity.

The number of adults obtained from the cultures on unshelled nuts (331) was significantly greater than that from shelled nuts (180) or from shelled nuts with shell added (231). The numbers emerging in successive two-day intervals from the three media are shown in fig. 2.

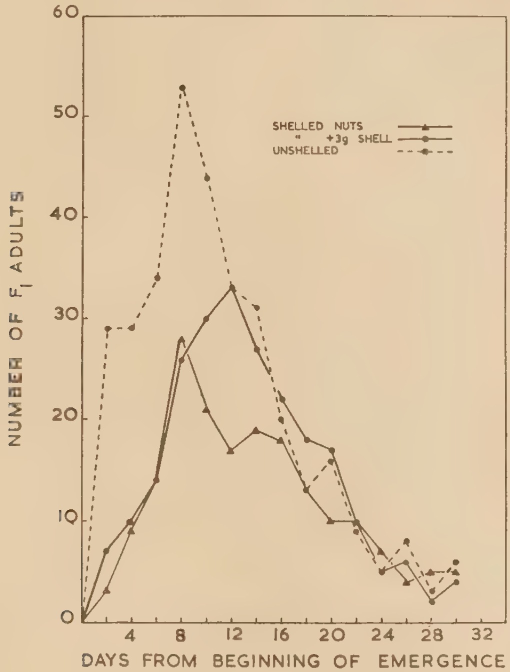

Fig. 2.—Numbers of F_1 adults of *C. gonagra* emerging in successive 2-day periods from cultures on different food media. Each value is the mean of two replicates (for details, see text).

There are three factors that might contribute to these differences:

(i) Eggs adhering to cracks on the irregular surface of the shell are better protected from damage than are those laid on the smooth testa of the kernel.

(ii) The large interstices between the unshelled nuts facilitate adult movement, resulting in a more even distribution of eggs and avoidance of overcrowding of the larvae (Prevett, 1954).

(iii) The microclimate produced by the larva in a kernel within a shell might be more uniform and therefore more conducive to its development than in a kernel without a shell. It is, however, unlikely that any differences as regards relative humidity that may occur between the larval microclimate in a shelled and an unshelled nut would affect development, since wide limits are tolerated (see Table VI).

Summary.

Information on the world distribution and host-plants of the Groundnut Bruchid, *Caryedon gonagra* (F.), has been summarised from the literature. As a

result of misidentification of the species that attacks groundnuts and of differing views about its generic assignment, this information has been given under several different names. The records brought together here are believed all to represent *C. gonagra*, and in a number of cases this has been confirmed by examination of the material concerned by Mr. B. J. Southgate.

C. gonagra is widely distributed in the Old World tropics and sub-tropics, but it is absent from Australasia, and it has only a restricted distribution in the New World tropics. Almost all its host-plants belong to the Leguminosae, the principal one being the tamarind, *Tamarindus indica*, in the pod of which the beetle has been found to develop more quickly than in the groundnut.

Data on the life-history and habits, and on the duration of pre-adult development and adult life, are summarised from the literature.

Experiments are described to determine the optimum conditions for multiplication of *C. gonagra*, using groundnuts as food. When adult females were allowed to lay large numbers of eggs on shelled and unshelled nuts, only a small proportion of the resulting larvae completed their development, the number of adults that emerged averaging about 2·4 per kernel in shelled nuts and 3·2 in unshelled ones. The developmental period at 70 per cent. relative humidity was 42 days at 30°C. and 91–98 at 25°C.; the former figure is less than any recorded in the literature at higher or lower temperatures, and all subsequent experiments were therefore made at 30°C. and 70 per cent. relative humidity.

Adults confined for three weeks, starting when four days old, at the rate of 25 pairs on 160 g. of a mixture of broken and intact kernels gave rise to some 314 F_1 adults; this total was virtually unchanged when 50 pairs were used, but lower densities, though giving rise to greater yields per parent adult, gave much lower yields per weight of food. Emergence of adults began six weeks after the date of egg-laying and reached its peak from one to three weeks later.

The yield from ten females on intact kernels was greater than from the same number on the mixture, but differed little whether the parent adults were left on for one week or three weeks, indicating that the majority of the eggs are laid in the first 11 days of adult life. The yield from unshelled nuts was nearly twice as great as that from shelled nuts, and also significantly larger than that from shelled nuts with ground shell added. Possible causes of this are discussed.

The sexes can be distinguished in the adult stage by differences in the terminal abdominal segments.

Acknowledgements.

Mr. D. W. Hall, Colonial Liaison Officer, Pest Infestation Laboratory, initiated the work and gave some help and criticism on the presentation of the paper. Thanks are due to Mr. P. F. Prevett, Stored Products Entomologist, Sierra Leone, for suggestions and for allowing his thesis to be referred to so freely. I also wish to thank especially the Commonwealth Institute of Entomology for much assistance, and Mr. B. J. Southgate, of this Laboratory, for permission to quote the results of his identifications of material.

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Appendix.

Identification of Males and Females of *C. gonagra*.

Males can be distinguished from females without the aid of a lens by differences in the last visible segments of the abdomen. Details are shown in fig. 3.

Male.—The pygidium or sixth visible tergite projects downwards, so that in dorsal view it is hidden by the elytra. The fifth visible sternite is deeply incurved anteriorly, so that the seventh tergite is often seen projecting between it and the pygidium.

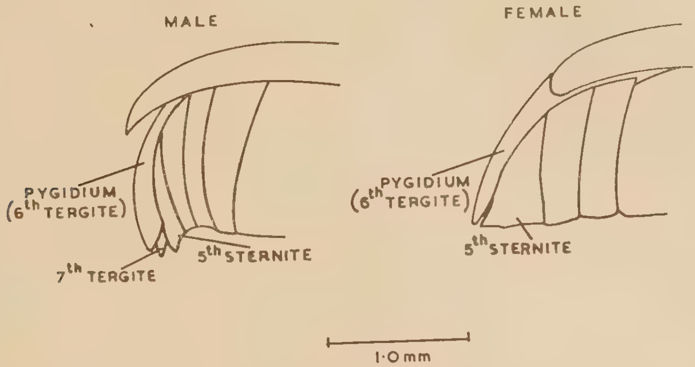

Fig. 3.—Abdomen of adult *C. gonagra*—lateral view, showing secondary sexual characters.

Female.—The pygidium can be seen in dorsal view projecting beyond the elytra. The fifth sternite is fully extended, so that the ventral surface is more or less flat. The seventh tergite is not represented in the female.

In other Bruchids, the sexes are often distinguished by a difference in the serration of the antennae, but in *C. gonagra* these are equally serrate in the two sexes.

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STUDIES OF BRITISH ANTHOMYIID FLIES.

IX.—BIOLOGY OF THE ONION FLY, *DELIA ANTIQUA* (MG.).

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In an account of the life-history of the Onion Fly (*Delia antiqua* (Mg.)) in England (Smith, 1922), it was stated that there were three generations a year and the approximate times for the appearance of each, calculated from observations on the first, were given. Maan (1945) stated that in Holland a third generation occurred only when there was hot weather in late summer and early autumn, and that some first-generation pupae did not give rise to flies until the following year. While rearing flies under laboratory conditions at Wye College, Miles (1955) found that in some seasons only a small proportion of first-generation pupae completed their development and gave rise to flies in the year in which they were formed. Among pupae formed from wild larvae taken in early July, about 20 per cent. in 1952 and 49 per cent. in 1954 passed immediately into the overwintering diapause. In laboratory cultures, 60 per cent. of the first-generation pupae entered a diapause in 1953 and over 90 per cent. in 1954. The frequency of diapause among first-generation pupae from laboratory cultures suggested that further study of the biology of the Onion Fly in relation to its environment was needed in order to obtain a better understanding of the annual cycle and to interpret correctly the observations made in the field.

Date of Emergence of overwintering Generation.

There have been few published records of the time of appearance of the overwintering generation in Britain and there has been no emphasis on these observations, and in consequence it has sometimes been assumed that the spring emergence of the Onion Fly occurs at approximately the same time as that of the Cabbage Root Fly (*Erioischia brassicae* (Bch.)). The writer has made no

TABLE I.

Peak periods of emergence of overwintering generation of *E. brassicae* and *D. antiqua* in the insectary.

Year	*E. brassicae*	*D. antiqua*
1953	1–9 April	1–7 May
1954	10–19 April	5–13 May
1955	—	19–27 May
1956	22–28 March	23 April–7 May

field observations on the Onion Fly because it has not been found on local crops during the period of these investigations, but insectary records (Table I) show that, in England, the Onion Fly emerges about a month later than the Cabbage Root Fly.

The times of emergence in an insectary are not necessarily the same as those occurring under natural conditions, but the observations of other workers have shown that the Onion Fly appears late in spring. In England, Smith (1922) first found the flies in the field on 30th May and Wright (1938) stated that the peak period of emergence was the last two weeks of May; in Holland, Maan (1945) found that the first flies appeared in the latter part of May; in Canada, Gibson & Treherne (1916) saw the first flies in the field in the third week of May, and Armstrong (quoted by Baker & Stewart, 1928) found them on 30th May; in Pennsylvania, Eyer (1922) recorded that adults began to emerge from overwintering puparia (presumably, in an insectary) on 4th May (1918), 29th May (1919) and 29th April (1920) and he gave 1st–10th June as the period of maximum oviposition in the field for the overwintering generation.

Preoviposition Period.

Previous workers (Eyer, 1922; Baker & Stewart, 1928) have stressed the importance of sunlight as a factor stimulating oviposition. In the course of observations at Wye, flies were bred for four generations in a constant-temperature room that was generally without light except that from a small, red, service lamp. This suggested that, although sunlight stimulated the flies to great activity (Baker, 1928), the heat factor was more important than the light factor in influencing the maturation of ova. At Wye, flies maintained at favourable temperatures but fed on sugar solution only, lived up to three months but did not lay eggs. Flies maintained at 6–8°C. and given food containing protein (milk) and carbohydrate (sugar) also laid no eggs although they survived up to four months. Flies fed similarly and maintained at higher temperatures laid eggs freely.

In captivity, the preoviposition period showed considerable individual variation. When maintained at 25°C. in relative darkness, the preoviposition period for seven flies was 10, 11, 14, 15 (2), 18 and 24 days, respectively, with an average of 15 days. At laboratory temperatures (12–29°C.) between 23rd April and 31st August, the preoviposition period for twelve flies was 10, 12 (4), 13 (2), 15 (2), 20 (2) and 25 days, respectively, again with an average of 15 days. At the lower temperatures that prevailed in the laboratory from October to March (11–20°C., with 15°C. predominating) the preoviposition period was 11, 12, 16 (2), 17, 18, 21 (2), 24 (2), 29 and 46 days, respectively, with an average of 21 days. These observations showed that low temperatures prolonged the preoviposition period. The observed preoviposition periods for spring and summer at Wye agree fairly well with those recorded by other workers: 10–14 days (Sanders, quoted by Gibson & Treherne, 1916); 11–25 days (Armstrong, quoted by Baker & Stewart, 1928); 7–21 days, with a general average of 10 days, and 10–15 days in the field (Eyer, 1922), and 12 days (van Emden, quoted by Kästner, 1929). These several observations would suggest that the preoviposition period of approximately seven days, which Smith (1922) determined by dissection, was an under-estimation that adversely affected his calculated times for the successive generations of the Onion Fly through the year.

Number of Eggs per Female.

At Wye, the numbers of eggs laid by individual flies showed great variation. The recorded totals for nine flies were 62, 92, 120, 68, 123, 39, 120, 10 and 39, respectively; and from two cages, each containing two pairs of flies, 193 and 187 eggs were obtained, an average of 95 eggs per female. These records agree fairly well with Kästner's observation (1929) that in captivity the number of eggs per female may be as high as 80; he estimated, however, that in the field the number was probably 40–50.

There was no discernible pattern of oviposition. The numbers of eggs laid by individual flies in the course of twenty four hours varied from 1 to 45, and batches of 40–45 eggs occurred seven times in the oviposition records of nine flies. This differs from a previous observation (Severin & Severin, 1915) that the number of eggs at one deposition was 1–15. The intervals between batches of eggs varied from 1 to 9 days and the duration of the oviposition period was from 7 to 25 days. This differs from the observations of Eyer (1922), who found that in laboratory cages the oviposition period was 4–5 days, and that eggs were laid at the rate of 7–9 per day with a complement of 30–40 eggs per female. In captivity at Wye, some unfertilised females laid eggs freely but the eggs did not hatch. Flies lived up to six days after laying their last batch of eggs.

Duration of imaginal Life.

Adults in captivity tended to have a long life. At 25°C., approximately 35 per cent., with males predominating, died during the first month; about 50 per cent. died during the second month, 11 per cent. during the third month, and the remaining two females were still laying eggs at the beginning of the fourth month when they were destroyed. Practically similar duration of imaginal life was observed when the overwintering generation was maintained at laboratory temperatures in spring and summer. Flies that were maintained under cooler conditions (autumn and winter laboratory temperatures) lived up to twenty one weeks. The long life in captivity has little direct significance, but taken with the long preoviposition period it suggests that the adults may have a long life in the field.

Incubation Period.

The rate of embryonic development depended upon temperature, and the eggs hatched under a wide range of temperature conditions. The incubation period for eggs at several temperatures is shown in Table II. Since eggs were collected from the cages once daily and afterwards examined once daily, the observed periods show no fractions.

TABLE II.

Incubation period of eggs of *D. antiqua* at various temperatures.

Temperature (°C.)	Period (days)
25	2
20 (approx.)	3–4
15 „	4–6
7–10 „	9–14

These incubation periods are somewhat similar to those given by Eyer (1922) who recorded 5·5 days at 60°F. (15·6°C.), 5 days at 69° (20·6°C.), 4·5 days at 70° (21·1°C.) and 3 days at 71° (21·7°C.); and by Baker & Stewart (1928) who give 4–6 days at 60°F. (15·6°C.), 3–5 days at 71° (21·7°C.) and 2·5–4 days at 75° (23·9°C.).

Duration of larval Stadia.

Larvae of the Onion Fly have three stadia. The first and second are short and approximately equal in duration; the third is longer and more variable. In

cultures at Wye, feeding and growth took place at temperatures ranging from 8 to 30°C. The duration of the several stadia at various temperatures are shown in Table III. Records of abnormally long periods in the several instars are omitted because the insects concerned failed to reach the imaginal stage.

TABLE III.

Duration of larval stadia of *D. antiqua* at various temperatures.

Stadium	Number of days at			
	9–11 °C.	14–16 °C.	19–21 °C.	25 °C.
First	8–12	4–6	3–4	2
Second ..	8–18	4–6	3–4	2
Third	24–37	15–24	8–14	5–9

Pupal Stage.

The duration of the pupal stage varied greatly because a pupal diapause frequently followed the development of larvae at temperatures below about 18°C. When the Onion Fly was reared at a constant temperature of 25°C., the pupal stage lasted 12–17 days; at approximately 20° it was 16–25 days, and at approximately 15° the majority of the pupae entered a diapause, and the pupal stage lasted from 35 days to over a year. These observations differed from those of Eyer (1922) who found that at an average temperature of 73°F. (22·8°C.) the pupal stage lasted 7–8 days; at 69° (20·6°C.) it lasted 9–10 days, and at 63° (17·2°C.) it lasted 14–15 days. The figures were, however, in general agreement with the pupal periods of 14–26 days recorded by Gibson & Treherne (1916), 16–19 days (Smith, 1922) and 14–18 days (Baker & Stewart, 1928).

Time required for Development from Egg to Adult.

Observations on the duration of the several stages gave a general notion of the time required for the development of the Onion Fly, but further information was deemed necessary in order to understand the annual cycle under field conditions. For this study, the eggs were kept in batches of about 10 in phials (3″ × 1″) and the larvae were fed on onion-leaf tissue. Filter paper was used in the phials to absorb excess moisture, as this had been observed to induce diapause in related Dipterous larvae (Wigglesworth, 1953, p. 81). Larvae were transferred to phials containing sand when they were ready to pupate. The phials were kept in a constant temperature maintained at 25°C. and at other temperatures in a multiple-temperature incubator.* The temperatures of the incubator were not constant, but varied somewhat with the temperature of the laboratory containing the apparatus. The times required for development from egg to adult at various temperatures are shown in Table IV.

Light conditions were not uniform. Larvae at 25°C. were maintained in relative darkness in a constant-temperature room; larvae in the multiple-temperature incubator had some light through a perspex cover, and those in the laboratory were shaded from direct light. The differences in effective light were probably small because all phials contained leaf tissue and filter paper, and the larvae fed within the pieces of leaf.

* Adapted by Dr. R. Dobson, now at Rothamsted Experimental Station, from the design of Williams & Kirkpatrick (1924).

Data in Table IV showed that the rate of development depended mainly upon the temperature. Baker & Stewart (1928) stated that heat retarded development in the Onion Fly but there was no evidence of this at the temperatures shown in the Table, and the one fly, a male, that completed its development in 22 days at the highest temperature shown in Table IV appeared normal. At 25°C., the Onion Fly was reared without the intervention of a pupal diapause for four generations, and it appeared that at this temperature there was no obligatory diapause. When the multiple-temperature incubator was unavoidably dismantled (13.viii.55) it was already apparent that diapause occurred when larvae were reared at the lower temperatures. Development from egg to pupa was successfully completed at a temperature as low as 9–10°C.

TABLE IV.

Development from egg to adult in *D. antiqua* at various temperatures.

Temperature (°C.)	No. flies reared	No. days required	Av. no. days	Distribution of frequencies
25–30	77	22–27	25	42 flies (54%) emerged in 25 days 59 flies (77%) emerged in 24–26 days
25	176	25–33	28	161 flies (90%) emerged in 26–30 days
22–27	215	25–36	30	176 flies (81%) emerged in 27–31 days
19–24	102	27–40	33	74 flies (72%) emerged in 31–34 days
16–21	36*	42–56	45	28 flies (76%) emerged in 42–46 days
12–15	1*	76	—	—
Lab. temp.† (mainly 15–25°C.)	186	29–45	35	140 flies (70%) emerged in 33–37 days

* Observations ceased unavoidably on 13.viii.55, before emergence was complete.
† Daily average about 20°C., but temperature occasionally rose to 30°, and night temperature sometimes fell below 15°.

Temperature associated with Diapause in pupal Stage.

Data on the duration of the pupal stage subsequent to rearing larvae at laboratory temperatures in late autumn and winter are given in Table V. The eggs were obtained from flies at 25°C. and from others at laboratory temperatures,

TABLE V.

Duration of pupal stage in *D. antiqua* under laboratory conditions.

Eggs laid	Temperature (°C.) (larval stages)	No. flies emerged	Duration of pupal stage (days) and period of emergence of flies*
27.x.55–5.xi.55	12–15	80	94–199 (4.iv.56–25.vi.56)
5.x.55–23.x.55	16–18	73	132–253 (5.iv.56–26.vii.56)
		12	no individual records (9.viii.56–4.x.56)
		6	394, 409 (2), 440, 434 and 442, respectively, (14.i.57–12.iii.57)

* See footnote to Table VI.

TABLE VI.

Duration of pupal stage when the pupae were maintained at a higher temperature than that at which the larvae developed.

Eggs laid	Temperature (°C.) (larval stages)	Temperature (°C.) (pupal stage)	No. of flies emerged		Duration of pupal stage (days) and dates of emergence period*
24.x.55 to 2.xi.55	Range 14–17	25	54	8	13–16 (12.xii.55 to 15.xii.55)
				46	94–208 (2.iii.56 to 24.vi.56)
3.v.56 to 30.v.56	Av. max. 18 Av. min. 10 (Insectary)	Av. max. 20 Av. min. 13 (July only)	322	37	25–35 (1.vii.56 to 27.vii.56)
				33	66–212 (10.viii.56 to 3.i.57)
				252	234–294 (4.iii.57 to 27.iv.57)
15.v.56 to 29.v.56	Av. max. 21 Av. min. 12 (Laboratory)	Av. max. 23 Av. min. 15 (July only)	283	30	21–31 (10.vii.56 to 20.vii.56)
				253	118–341 (19.x.56 to 6.vi.57)

* Since the eggs were not all collected on the same day and since the duration of the egg–pupation period was variable, the difference between the first and last dates of emergence and the interval in the number of days shown for the duration of the pupal stage do not necessarily correspond. The dates of emergence are not necessary to the Table, but serve to show that there was a tendency for the majority of the flies to emerge in spring, even under the modified seasonal temperature rhythm of a field laboratory.

but the environment of the adults before and during oviposition had no observable influence on the larval and pupal development of their progeny. The larvae were reared in two sites, a south-facing laboratory where the temperature was mainly 16–18°C., but occasionally rose above 22° on sunny days and on cold nights fell to 12°, and a north-facing laboratory where the temperature was generally about 3° lower. The development from egg to pupa required 26–34 days at the higher temperature and 30–37 days at the lower. During larval development and after pupation, the temperatures tended to fall slightly. All the pupae entered a diapause and the emergence of flies began after the temperature rose slightly in spring.

The threshold temperature for pupal development was not known, and no distinction could be made in Table V between pupal diapause induced by the environment of the larvae and that associated with the environment of the pupae. Evidence that the larval environment was a major factor in causing diapause in the pupae was obtained by transferring newly-formed puparia from the laboratory to a constant temperature of 25°C., at which the duration of the pupal stage, following larval rearing at that temperature, was 12–17 days (p. 408). The results, given in Table VI, show that only 15 per cent. (8) of the pupae from larvae reared at 14–17°C. continued their development at 25°C. without a diapause and gave rise to flies in 13–16 days; the remaining 85 per cent. (46) entered a diapause that prolonged the pupal stage to 94–208 days at 25°C.

The frequency of diapause in pupae from larvae reared in early summer under laboratory and insectary conditions (Table VI) seemed to be the result of the temperature at which larval development took place. The insectary temperatures corresponded closely with the air temperatures recorded at the Wye meteorological station about 200 yd. away. Pupae from insectary-bred larvae were exposed to temperatures generally higher than those obtaining during larval development but only 11 per cent. (37) gave rise to flies in July after a pupal period of 25–35 days. The remaining pupae entered a diapause of varying length. Laboratory temperatures were slightly higher than those of the insectary, but in laboratory cultures also most of the pupae entered a diapause, and only 11 per cent. (30) gave rise to flies in July after a pupal stage lasting 21–31 days. Baker & Stewart (1928) noticed the occurrence of retarded development in pupae of the Onion Fly and they associated it with hot, dry, summer weather, but the frequency of pupal diapause under the moderate temperatures shown in Table VI and the rapidity with which the life-cycle was completed at 25–30°C. (Table IV) showed that, under conditions at Wye, the chief factor associated with retarded pupal development was the temperature at which larval growth took place.

The times for the emergence of flies from pupae in diapause under insectary and laboratory conditions, respectively, showed differences. In the insectary, where the pupae were exposed to seasonal changes of temperature, 33 flies emerged before the onset of winter; of these, 16 emerged between 10th August and 10th October (the dates are not known), 11 emerged from 11th–25th October and 6 emerged from 1st November to 3rd January. The remaining 252 gave rise to flies in the following spring during March and April after pupal periods varying from 234 to 294 days, and all except 12 flies emerged in a peak period lasting from 21st March to 27th April. Pupae in diapause in the laboratory were seldom exposed to temperatures of less than 12°C. The emergence of flies took place over several months, after pupal periods that varied in duration from 118 to 341 days. There was no well-defined peak period of emergence of 253 flies that emerged from 19th October to 6th June, 4 emerged in October, 13 in November, 14 in December, 29 in January, 48 in February, 63 in March, 45 in April and 37 in May and early June.

Conclusions.

Rearing the Onion Fly at various temperatures in the laboratory and insectary has shown that diapause in the pupal stage is not obligatory, since, at 25°C., four generations were reared without the intervention of diapause, whereas, at lower temperatures, diapause occurred.

It was not possible to ascertain the lowest temperature that permitted continuous development, but the individual differences in the development of the flies under observation suggested that there might be no well-defined level of temperature above which breeding was continuous and below which pupal diapause invariably occurred. Nevertheless, it was found that, when larvae were exposed to certain general temperature conditions during their development, a high proportion of the subsequent pupae entered diapause; thus, below 18°C., the species was mainly univoltine. Since pupal diapause was induced by these temperatures at various times of the year, it appeared that other environmental factors such as light intensity, humidity and larval food were not important.

If pupae obtained from larvae reared under cool conditions were exposed to a higher temperature, their rate of development was not accelerated, nor was it necessary to expose them to low temperatures in order to break the diapause.

When pupae in diapause were exposed to seasonal temperatures their subsequent development tended to be uniform, and the adults showed a peak period of emergence. When the diapause broke without exposure to cold, the emergence of the adults took place over several months, without a marked peak.

It has not been possible to correlate the temperatures that have been associated with pupal diapause under laboratory conditions with the temperatures of the zone naturally inhabited by larvae of the Onion Fly. The latter vary with the character and condition of the soil, the density of the crop, and the rainfall and hours of sunshine. Maan (1945) observed diapause in first-generation pupae in Holland, and it seems probable that field observations would show that the phenomenon also occurred elsewhere. It would also appear that the number of generations per annum and the fly population in late summer and autumn are determined largely by weather conditions in June and early July when first-generation larvae are feeding and not, as has been generally suggested, by the weather in late summer and early autumn.

Summary.

The Onion Fly (*Delia antiqua* (Mg.)) was bred at Wye, Kent, under insectary and laboratory conditions to obtain further information on its biology and reactions to various temperatures.

A comparison of the times of emergence of overwintering generations of Onion Fly and Cabbage Root Fly (*Erioischia brassicae* (Bch.)) in an insectary showed that the former emerged consistently about a month later than the latter. This supported the observations of previous workers that the Onion Fly was not active in the field until late May.

A diet containing protein was necessary for oviposition. The length of the preoviposition period was affected by temperature. Flies maintained at 25°C. laid eggs in 10–24 days, with an average of 15 days. At spring and summer laboratory temperatures (12–29°C.) the preoviposition period was 10–25 days, with an average of 15 days; and in autumn and winter (11–20°) it was 11–46 days with an average of 21 days. Flies maintained at 6–8° did not lay eggs.

Flies in captivity laid up to 123 eggs at the rate of 1–45 per day. Intervals between batches of eggs varied from 1–9 days, and the oviposition period was 7–25 days. Flies lived up to 6 days after oviposition.

The incubation period depended on the temperature. Eggs at 25°C. hatched in 2 days; at 20° in 3–4 days; at 15° in 4–6 days; and at 7–10° in 9–14 days.

The temperature also affected the duration of larval and pupal stages. At 25°C. the successive larval stadia required 2, 2 and 5–9 days, respectively. Lowering the temperature increased the time for development until at 9–11° the three larval stadia required 8–12, 8–18 and 24–37 days, respectively. At 25° the pupal stage lasted 12–17 days; at 20° it was 16–25 days, and at 15° it was from 35 days to over a year. At 25–30° the development from egg to adult was completed in 25 days; at 25° it required 28 days; at 22–27°, 30 days; at 19–24°, 33 days.

At 25°C. the Onion Fly bred continuously without diapause. When larvae were reared at temperatures below about 18° pupal development was often retarded. Pupae formed from larvae reared at 12–18° and maintained at approximately that temperature, required 94–442 days to complete their development. By raising the temperature of pupae formed from larvae reared below 18°, it was demonstrated that a true diapause had been induced. Of 54 pupae raised to 25°, 8 (15%) completed their development in the expected time (13–16 days) and 46 (85%) required 94–208 days. Of 322 pupae formed from larvae reared in an insectary in May and June at 10–18° and exposed to July temperatures of 13–20°, 37 (11%) emerged in 25–35 days and 252 (78%) required 234–294 days. Similarly, of 283 pupae formed from larvae reared at 12–21° and exposed to a temperature of 15–23°, 30 (11%) completed their development in 21–31 days while 253 (89%) required 118–341 days. Exposure to low temperatures was not necessary to terminate pupal diapause.

Acknowledgements.

The writer thanks the Principal and Governors of Wye College for facilities for the work and the Royal Society for a grant for thermographs. She gratefully acknowledges the helpful criticism of Professor H. W. Miles in whose department the work was done. She also thanks Professor R. L. Wain for permitting her to use the constant-temperature room of his department, and Mr. B. Emmett for his help with the cultures of the Onion Fly.

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MALES OF *CULICOIDES ANOPHELIS* EDW.

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Culicoides anophelis Edw. is of wide occurrence in India, Ceylon, Burma, Malaya, Thailand, Indo-China, Sumatra, Tonkin, and as far as New Britain (Laird, 1946). From India the species has almost invariably been obtained in the act of engorging on female mosquitos, mostly Anophelines (*A. annularis* Wulp, *A. hyrcanus nigerrimus* Giles, *A. barbirostris* Wulp, *A. subpictus* Grassi, *A. vagus* Dön., *A. aconitus* Dön. and *A. maculatus* Theo.). But the species may also attack members of the Culicini, as observed by Fearnside (1900) in the case of certain unidentified examples of the genus *Culex*. We have also observed the species attacking *Culex pipiens fatigans* Wied. and *Mansonia* (*Mansonioides*) *annulifera* (Theo.), which suggests that the occurrence of the species is not so uncommon on members of the Culicini as was thought previously. The reason for the missing of the association of the species with the latter group of mosquitos by most workers seems to lie in the fact that the Culicini were not examined previously in large numbers (Edwards, 1922).

Edwards' (*loc. cit.*) description of the species *Culicoides anophelis* is based on females only. Males of the species were not known to him, nor had they been discovered by others since. We have, however, collected a few males from the environs of Calcutta which we consider to be those of *C. anophelis* on grounds of

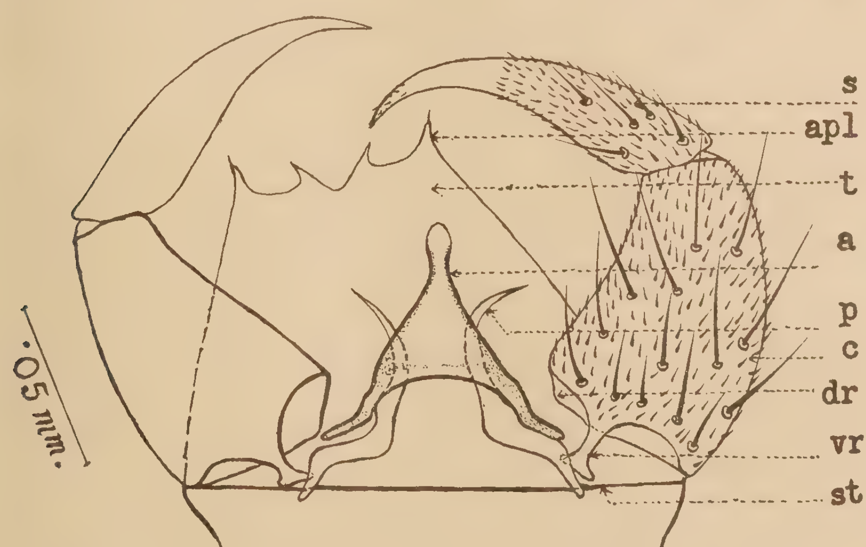

Fig. 1.—Hypopygium of *Culicoides anophelis*: a, aedeagus; apl, apico-lateral process; c, coxite; dr, dorsal root of coxite; p, paramere; s, style; st, ninth sternite; t, ninth tergite; vr, ventral root of coxite.

taxonomic similarity with the description of Edwards. The characters of these males are given below:

The antennae plumose, tufts having shiny yellowish appearance. Thoracic pattern as in the female; wings 0·9 mm. long and 0·3 mm. broad with very few hairs. In other respects the wings resemble those of the female, as do the halteres.

Hypopygium (fig. 1): Ninth sternite (st) flat; ninth tergite (t) prominently notched in the middle, the edges of notch are prolonged into sharp-pointed structures, the apico-lateral (apl) process on either side blunt, tipped with a short spine. Ventral root (vr) of the coxite (c) somewhat footlike, the dorsal root (dr) blunt and inconspicuous. Style (s) curved inwards tapering to a point distally, clothed on basal half with fine spines interspersed with a few hairs while the tip is provided with a few short spines. Parameres (p) distal portion long, narrow, tapering to a filiform end, and strongly curved outwards; proximal part bare, strongly chitinised, also curved outwards. Aedeagus (a) inverted "Y"-shaped with the stem ending in a delicate membranous knob. Membrane connecting the aedeagus with ninth tergite studded with spines.

Male measures approximately 1·2 mm. in wet preparation. Slide preparations of specimens are deposited with the Zoological Survey of India, Calcutta.

Some doubts as to the systematic status of *Culicoides raripalpis* Smith, which has a similar distribution to that of *C. anophelis*, have been raised by Macfie (1932), who felt that, on the evidence of a similarity in the spermathecae, the former might be a variety of *C. anophelis*. The male of *C. raripalpis* has since been described and figured by Causey (1938). It is therefore of interest to note if there is any similarity between the present description and that of Causey for *C. raripalpis*. On comparison of Causey's figure of the male terminalia of *C. raripalpis* with our fig. 1 we find, however, that the ninth tergite in the two differs greatly: while in *C. raripalpis* it bears an apico-lateral process on either side, in *C. anophelis* there is a pair of additional projections, those bordering the central notch, in between the apico-lateral processes. Moreover, the aedeagus terminates in a knob in *anophelis* in contrast to the blunt flat tip described in *raripalpis*.

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TAXONOMIC NOTES ON *LEUCOPTERA MEYRICKI* GHESQUIÈRE AND *LEUCOPTERA COFFEELLA* (GUÉRIN-MÉNEVILLE) (LEPIDOPTERA, LYONETIIDAE).

By J. D. Bradley

Department of Entomology, British Museum (Natural History).

These notes are intended primarily to bring to notice the correct name and identity of the species of Lyonetiid moth occurring as a leaf-mining pest of the coffee plant in East Africa that has for a long time mistakenly gone under the name of *Leucoptera coffeella* (Guér.). A recent survey of East African material standing under the name *coffeella* in the British Museum collections, and material received from the Commonwealth Institute of Entomology collected in Kenya and Tanganyika in 1957, has not yielded one specimen of the true *coffeella* from this part of the world. The East African species that has unfortunately become generally accepted as *coffeella*, and referred to as this species in the economic literature, should properly go under the name *Leucoptera meyricki* Ghesq.

Leucoptera meyricki Ghesquière.

Leucoptera meyricki Ghesquière, 1940, Ann. Mus. Congo Belge, Tervuren, Ser. III (II) **7,** fasc. 1 p. 80.

Leucoptera coffeella (Guér.) Meyrick *nec* Guér., 1922, Exotic Microlepidoptera, **2,** p. 557.

This species was for a good many years believed to be *Leucoptera coffeella* and seems to have remained under this name until the Belgian entomologist Ghesquière (*op. cit.*) gave it the new trivial name *meyricki*. When proposing this name, Ghesquière referred to six specimens from Kabete, Kenya, collected by H. E. Box in 1922, that had been identified as *coffeella* by Meyrick (*op. cit.*) and used by the latter for redescribing that species. Five of these specimens in the British Museum are collectively syntypes of *meyricki*, since a type was not indicated for this species by Ghesquière. I have now selected and labelled a specimen as lectotype with the following specification: ' a male, glued to a celluloid point; pinned to the point is a small rectangular white label bearing data in Meyrick's handwriting, "Kabete, Kenya Col. B. bred 1.22" '. This specimen is one of two syntypes that came to the British Museum in Meyrick's collection, identically mounted and labelled, and determined as *coffeella* Guér. The right-hand wings of the second specimen have been removed and were probably mounted by Washbourn on his slide preparation "RW 24". Three other syntypes were already in the British Museum and are individually mounted on polyporus and labelled with printed Museum data labels giving essentially the same data as that on the lectotype. One of the series is, however, represented by the pin and label only, the specimen having evidently at some time become detached from its pin and lost. In the British Museum, there is no sixth specimen in the syntype series, but there is a specimen with the same data, which was mentioned by Washbourn (1940, p. 456, para. 3, section (b)) as standing under the name *Leucoptera daricella* (Meyrick). This has been found on re-examination to be *meyricki*. It is a female and the genitalia are mounted on slide 1276 and the left-hand forewing on a second slide likewise labelled 1276.

Life-history: The bionomics of *meyricki* have been described in detail under the name *Leucoptera coffeella* by Box (1923) and Notley (1948 & 1956), and the

latter author has also compared them with those of another East African species, *L. caffeina* Wshbn.

Distribution: Kenya and Tanganyika. It remains to be proved whether or not records of *coffeella* from Ceylon, Madagascar and elsewhere in the Old World are correct or whether they refer to *meyricki* or some other species.

Leucoptera coffeella (Guér.).

Elachista coffeella Guérin-Méneville, 1842, Mém. Ins. Cafiers Antilles, p. 15, 2 pls. Paris.

The erroneous determination of the East African species mentioned above has led to reports in the literature of *coffeella* occurring in Kenya and Tanganyika, and specimens from these countries consequently probably stand wrongly labelled as *coffeella* in collections. So far as it has been possible to establish from a comparative study of available material the true *coffeella*, the larvae of which are also leaf-mining pests of the coffee plant, is a Neotropical species and is not found in East Africa. Records from Ceylon, Madagascar, Réunion, Mauritius and elsewhere in the Old World would best be regarded as doubtful until reinvestigated.

The situation regarding the identity of *coffeella* is complicated by the fact that the type material of this species cannot be traced and probably no longer exists, and by the general scarcity of authentic material from the West Indies in the Museum collections. In fact, the present determination of this species is based almost entirely on a series of specimens from Trinidad bred from *Coffea canephora* in April 1957 by Prof. T. W. Kirkpatrick. This material agrees fairly well with the figures given by Guérin (*op. cit.*) but the determination should perhaps be viewed with caution for the time being, since the wing venation differs markedly from that depicted for *coffeella* by Silvestri (1943, fig. 237), the differences being sufficiently great to suggest that more than one species may be involved. The illustration of the wing venation given with the original description by Guérin (*loc. cit.* pl. 1, fig. 9) seems to be incomplete and is of little use. A feature of considerable interest is that the East African *meyricki* and the Trinidad specimens believed to be *coffeella* are not only similar superficially but have a similar wing venation and morphological structure of male and female genitalia, and are evidently very closely related species.

Life-history: Guérin-Méneville & Perrottet (1842); Mann (1872) and Silvestri (1943, pp. 194–196).

Distribution: West Indies and certain coffee-growing areas in South America. Records elsewhere would best be regarded as doubtful until confirmed.

Some Remarks on the Present Generic Assignment.

The general practice has been followed in retaining *meyricki* and *coffeella* in the genus *Leucoptera* Hübner, but the generic position of these species requires more thorough investigation. The two species are closely related and are unquestionably congeneric, but both show certain differences in wing venation, morphology of male and female genitalia and spining of the abdomen from *Leucoptera spartifoliella* (Hübner), the type species of the genus, which may be of generic importance. They belong, however, to a complex of species that needs to be studied as a whole before the taxonomic importance of these differences can be properly evaluated. Silvestri (*op. cit.*) erects the apparently new genus *Perileucoptera* for *coffeella*, which is in all probability perfectly tenable; but in view of the disparity between his figure of the wing venation and the wing venation of the Trinidad material mentioned above, this genus has not been adopted lest there has been some confusion over the species.

Summary.

Records of *Leucoptera coffeella* (Guér.) from Kenya and Tanganyika have been found to be based on misidentifications and to refer to a distinct species, *Leucoptera meyricki* Ghesq. Other records of *coffeella* from the Old World seem open to doubt and require to be reinvestigated since they may also be based on misidentifications. *L. coffeella* seems likely to be a Neotropical species predominant in the West Indies. A lectotype is designated for *meyricki*, but the type material of *coffeella* cannot be traced and the identity of the latter species remains to be properly established. The present generic assignment of *meyricki* and *coffeella* in the genus *Leucoptera* Hübn. needs to be reconsidered in the light of the new genus *Perileucoptera* Silvestri (1943).

Acknowledgements.

The present investigation has been possible through the efforts of the Commonwealth Institute of Entomology, London, in obtaining freshly collected material from Prof. T. W. Kirkpatrick, Imperial College of Tropical Agriculture, Trinidad, Dr. H. C. James, Department of Agriculture, Jamaica, Mr. D. J. McCrae, Coffee Research Station, Ruiru, Kenya, and Mr. R. G. Tapley, Coffee Research and Experiment Station, Lyamungu, Tanganyika, to all of whom we are much indebted.

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AN ACCOUNT OF THE WEEVIL LARVAE BRED FROM THE BANANA PLANT IN UGANDA, WITH A DESCRIPTION OF THE LARVA OF *TEMNOSCHOITA NIGROPLAGIATA* (QUED.) (COL., CURC.).

By Paul E. S. Whalley, B.Sc., F.R.E.S.
Department of Agriculture, Uganda.

The life-history of the Banana Weevil, *Cosmopolites sordidus* (Germ.), has been described many times (Ghesquière, 1927; Froggatt, 1928; Harris, 1947; Cuillé, 1950). The eggs of this weevil are laid either in the base of the living pseudostem of the banana plant or in the cut pseudostem lying on the ground. On hatching, the larvae tunnel into the rhizome and may cause serious damage to the living plant and affect the subsequent yield of fruit.

It has been known for some time that species of the genus *Temnoschoita* Chevr. were associated with rotting pseudostems (Hargreaves, quoted in Marshall, 1938). Hargreaves (unpublished observation) says that the larvae of *Cosmopolites* and *Temnoschoita* are similar, and Alibert (1938) gives a brief description of the larva of *T. quadripustulata* (F.), which he states will attack the banana plant as well as the oil palm, in which it usually develops.

During the course of a recent survey of the distribution of *C. sordidus* in Uganda, larvae of *T. nigroplagiata* (Qued.) were found in living pseudostems of banana in West Nile, Toro and Bugisu Districts.

It is important to distinguish the larvae of these two genera of weevils. Identification of banana weevil (*i.e.*, *C. sordidus*) in the field in Uganda is often based on the presence of larvae in the pseudostem without recourse to the adults.

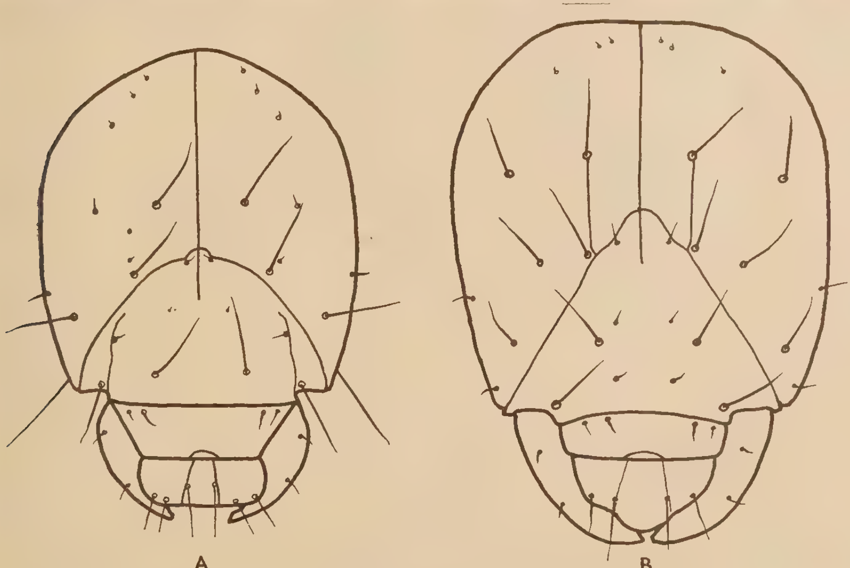

Fig. 1.—Head capsule of full-grown larva: anterior view of (A) *T. nigroplagiata*, (B) *C. sordidus*.

The adults themselves are easily distinguished, *T. nigroplagiata* having orange markings on the thorax and elytra and *C. sordidus* being all black. Although *T. nigroplagiata* usually breeds in rotting stems, it can attack living stems.

In the Western Province of Uganda, *C. sordidus* is absent from the vicinity of Fort Portal and the southern part of Kigezi and it is found only in the southern half of the West Nile District (Northern Province). Otherwise it has spread throughout Uganda.

T. nigroplagiata is found in every banana-growing area in Uganda and is particularly abundant in those where *C. sordidus* is absent (Fort Portal) or rare (West Nile). Other species of *Temnoschoita* associated with the banana plant are *T. basipennis* Duv. and *T. erudita* Duv. The larvae of the former have been bred from rotting pseudostems but are not common and in recent years have been recorded only from Western Province. There is one specimen in the collection of the Department of Agriculture, Kawanda, labelled "Entebbe, G. C. Gowdey 1909". *T. erudita* has only been found in the adult state in Bwamba, Western Province.

A full account of the larva of *C. sordidus* is given by Anderson (1949). Only two larvae of *T. basipennis* have been examined and these varied slightly in structure so that it has not been possible to separate this species from *T. nigroplagiata*. The following description of the full-grown larva of *T. nigroplagiata* follows the terminology used by Anderson (1947, 1949) except that, as regards the spiracles, the term "air-tubes" is not used and "septum" describes the partition visible externally in the spiracles.

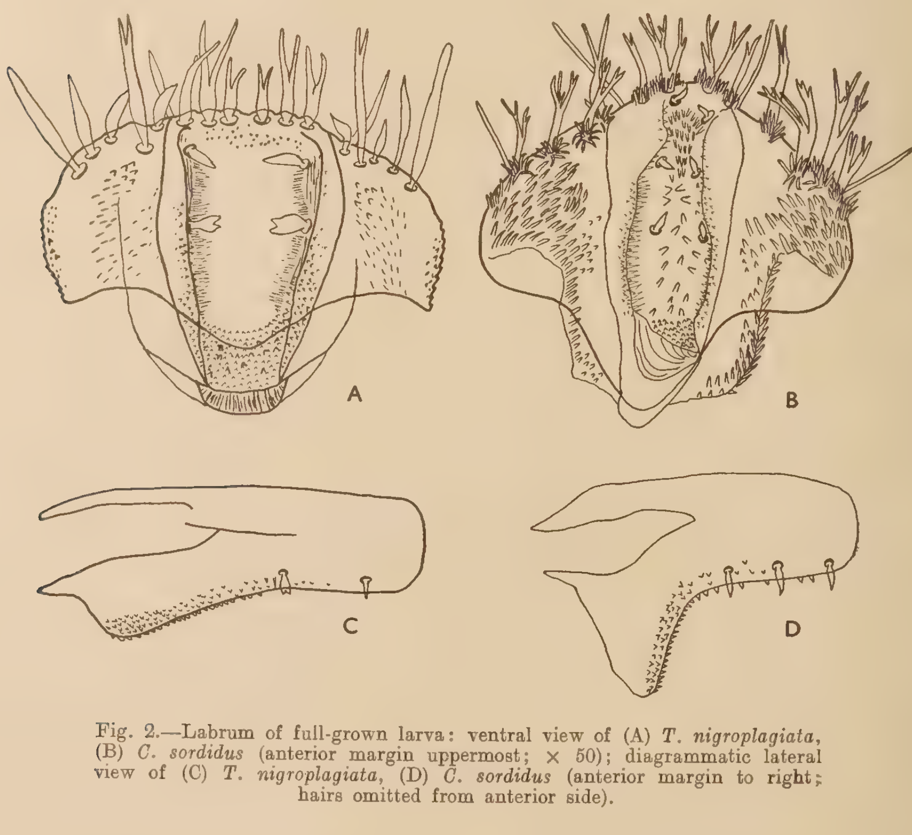

Fig. 2.—Labrum of full-grown larva: ventral view of (A) *T. nigroplagiata*, (B) *C. sordidus* (anterior margin uppermost; × 50); diagrammatic lateral view of (C) *T. nigroplagiata*, (D) *C. sordidus* (anterior margin to right; hairs omitted from anterior side).

Description of the Larva of *Temnoschoita nigroplagiata.*

Head free, light orange-brown, darker on the frons, clypeus and labrum. Ocelli absent. Labrum with one basal and two lateral sensillae. Mala with three ventral setae (outer ones branched) and eight dorsal setae (all branched). Asperities on mala on dorsal surface round the base of the setae; setae 7 and 8 usually with asperities small or absent. Mandibles with broad apical tooth indented. Endocarina present, one-third to one-half as long as the frons. Labral rods convergent but not united posteriorly. Epipharynx with all the antero-median setae and one pair of antero-latero setae two-branched. Two pairs of median setae on the epipharynx with the posterior pair often bifurcate. Ligula not produced, with asperities on its anterior margin.

Thoracic spiracle $1\frac{1}{2}$ times as large as the abdominal ones. Setae of epipleuron of meso- and of meta-thorax long.

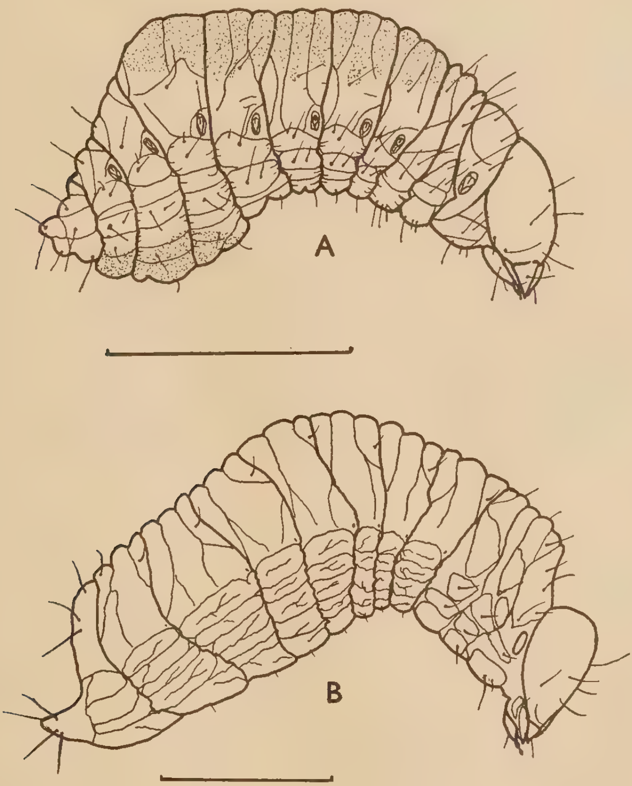

Fig. 3.—Full-grown larva, lateral view: (A) *T. nigroplagiata*, (B) *C. sordidus.* Length of line 0·5 cm.

Spiracles on abdominal segments I–VII clearly visible, with a small septum on the dorsal side. Abdominal segment VIII with spiracles reversed and the septum on the ventral side. Abdomen with minute spines on the dorsal side of segments I–V (inclusive) and on the ventral side of V–VII (inclusive). Macroscopically these give the impression of dark areas on the larva.

The larvae vary in length from 1·2 mm. (mean head width 0·3 mm.) (1st instar) to between 12 mm. and 15 mm. (mean head width 2·5 mm.) when fully grown.

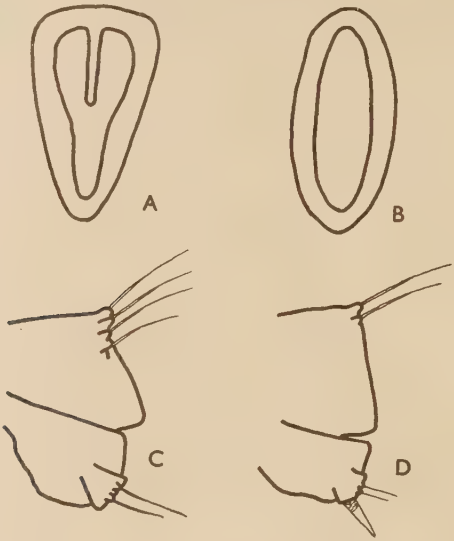

Fig. 4.—A, B. Full-grown larva: diagram of thoracic spiracle of (A) *T. nigroplagiata*, (B) *C. sordidus*. C, D. Pupa: lateral view of last abdominal segment of (C) *T. nigroplagiata*, (D) *C. sordidus*.

Characters separating the immature Stages of *T. nigroplagiata* from those of *C. sordidus*.

The following characters, based on those of the full-grown larvae and the pupae, can be used to separate *C. sordidus* and *T. nigroplagiata* (those marked * can be used in the field with a × 10 lens). This key supersedes a shorter, earlier version (Whalley, 1957).

Larva

Temnoschoita nigroplagiata	*Cosmopolites sordidus*
* 1. Head rounded, ovate in outline when viewed anteriorly (fig. 1, A).	1. Head "squareish" in outline when viewed anteriorly (fig. 1, B).
2. Labrum flattened at anterior margin (fig. 2, A).	2. Labrum with anterior margin more pointed (fig. 2, B).
3. Median setae on anterior margin of labrum mainly bifid (fig. 2, A).	3. All setae on anterior margin of labrum many-branched (fig. 2, B).
4. Posterior margin of labium rounded.	4. Posterior margin of labium pointed.
5. Setae on dorsal side of mala of labium mainly bifid.	5. Setae on dorsal side of mala many-branched.
6. Thoracic and abdominal spiracles with partial septum (fig. 4, A).	6. Spiracles simple (fig. 4, B).
* 7. Abdomen with 8 pairs of spiracles, of which the anterior 7 visible laterally (fig. 3, A).	7. Abdomen with 8 pairs of spiracles, of which the anterior 7 rudimentary and not easily visible laterally (fig. 3, B).
8. Abdomen with microtrichia on dorsal side of segments 1–5 and ventral side of segments 5–7.	8. No microtrichia.
* 9. Abdomen tapering gradually from the 5th segment posteriorly (fig. 3, A).	9. Abdomen not tapering gradually, 5th segment abruptly scooped out (fig. 3, B).
10. Ventral side of labrum not humped posteriorly (fig. 2, C).	10. Ventral side of labrum humped posteriorly (fig. 2, D).

Pupa

Temnoschoita nigroplagiata	*Cosmopolites sordidus*
* 1. Cocoon always present.	1. Cocoon almost always absent.
* 2. Last abdominal segment with two fine ventral spines on each side (fig. 4, C).	2. Last abdominal segment with one large and two fine ventral spines on each side (fig. 4, D).
* 3. Dorsal side of last abdominal segment with 8 papillae, each bearing a single spine (fig. 4, C).	3. Dorsal side of last abdominal segment with 4 papillae, each bearing a single spine (fig. 4, D).
4. Spines on raised papillae dorsal to each abdominal spiracle.	4. No papillae, spines small.

Summary.

The two weevils associated with the living stems of the banana plant in Uganda are *Cosmopolites sordidus* (Germ.) and *Temnoschoita nigroplagiata* (Qued.); the damage caused by the former has been known for many years but the latter, which usually breeds in rotting stems, has only recently been shown to attack living ones. *T. nigroplagiata* occurs in every banana-growing area in the territory and is particularly abundant in some parts of western Uganda where *C. sordidus*, which is otherwise widespread, is rare or absent. Other species of *Temnoschoita* associated with the banana plant that occur in Uganda but that are rare, are *T. basipennis* Duv., bred from larvae in rotting pseudostems, and *T. erudita* Duv., known only from the adult.

The full-grown larva of *T. nigroplagiata* is described in detail and characters are given for separating the larva and pupa of this species from those of *C. sordidus*.

Acknowledgements.

The assistance and advice of Mr. J. Bowden, Senior Entomologist, Mr. J. C. Davies, Entomologist, and Mr. T. R. Odhiambo, of the Kawanda Research Station, and Mr. A. R. Dunbar, of Arua, is much appreciated. Dr. F. van Emden, of the Commonwealth Institute of Entomology, read the draft and made valuable criticism for which I am extremely grateful. Permission to publish this paper has been given by the Director of Agriculture, Uganda.

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AN ATTEMPT TO ERADICATE *GLOSSINA PALPALIS* (R.-D.) AND *G. TACHINOIDES* WESTW. FROM RIVERINE VEGETATION IN BENUE PROVINCE, NORTHERN NIGERIA, BY SPRAYING WITH DDT.

By J. B. Davies

Entomologist, Sleeping Sickness Service, Medical Department, Northern Region, Kaduna, Nigeria.

(Plate XV.)

Because of the increasing high cost of labour, during recent years, the eradication of *G. palpalis* (R.-D.) and *G. tachinoides* Westw. from the riverine vegetation by the normal method of partial clearing in Benue Province was rapidly becoming uneconomic. In consequence, the Sleeping Sickness Service of the Medical Department of Northern Nigeria decided in January 1955 to conduct a field trial, on the same general lines as those used in Kenya (Wilson, 1953), using DDT as a method of eradication. The objects of the trial were two-fold, namely, to determine if such a method was effective, and to evolve a suitable technique.

General Description of the Site.

For this trial, two tributaries of the River Konshisha, the Abeba and Avende, were chosen as being convenient, typical of the area and of reasonable length.

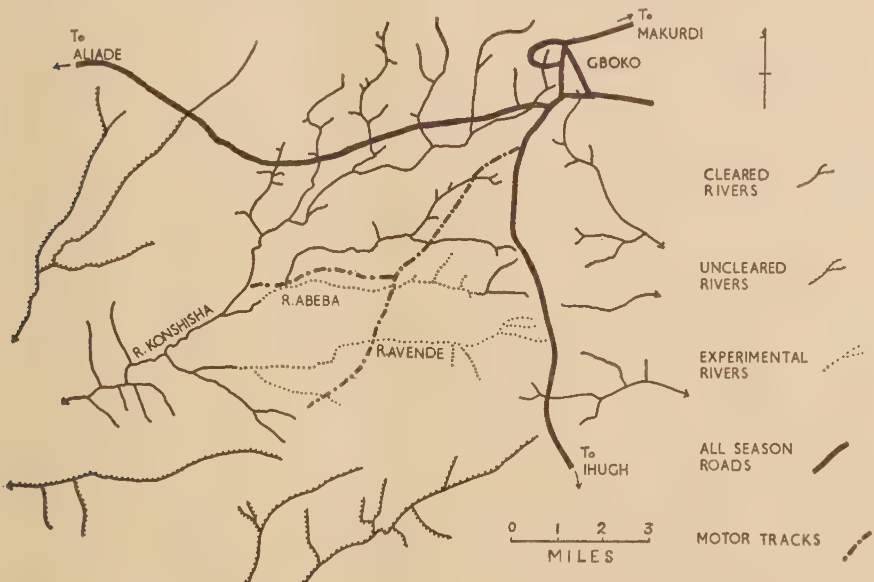

Fig. 1.—Map showing the position of the experimental rivers (dotted lines), in relation to the cleared rivers (continuous lines).

The River Konshisha rises close to Gboko in the Benue Province of the Northern Region of Nigeria (Lat. 7°20′N., Long. 8°55′E.) and flows southwards to join the Cross River system.

The general vegetation type is that described by Keay (1949) as Southern Guinea Savannah Zone, but in the vicinity of these rivers the land has been extensively farmed so that the country between and around them is open for the greater part of the year and only supports any considerable vegetation at the end of the rains when the cassava, guinea corn and benniseed crops are ready for harvesting.

Climatically, the area has well-defined wet and dry seasons, the dry season lasting from about November until March with perhaps one or two thunderstorms in late January but otherwise devoid of rain. Towards the end of December there is usually a period of three weeks or so during which a cold, dry wind or "Harmattan" blows from the north, bringing with it cold nights and mornings with occasional heavy dew in the valley bottoms and a dust haze during the remainder of the day. The wet season lasts from March to November, during which the rainfall totals between 40 and 50 in. Due to the porous nature of the soil, this rain does not run off the surface to form erosion gullies as it does further north, but sinks in, forming a relatively high water-table so that the majority of rivers contain running water all the year round. This constant flow of water supports the rain-forest type of vegetation which forms large strips of forest along the course of the rivers, in places reaching up to 1,000 yd. in width. An idea of some of the vegetation can be gained from Plate XV.

Description of the Rivers.

It can be seen from figs. 1 and 2 that the two rivers lie roughly parallel. They are separated by open farmland, the shortest distance between them being $\frac{7}{8}$ mile in the vicinity of the motor track (fig. 2). The rivers were isolated from

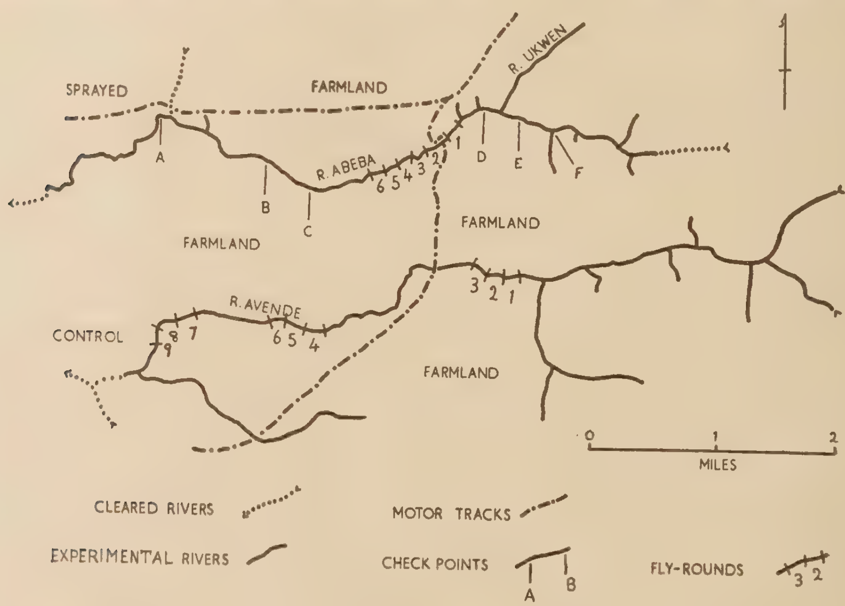

Fig. 2.—Map showing details of fly-rounds and check points on the experimental rivers (here shown by continuous lines). Fly-round sections are indicated by numbers, and check points by letters. Cleared stretches of rivers are shown by dotted lines.

each other by extending the existing clearing programme * to include the whole of the River Konshisha system adjacent to the rivers. The rivers were further isolated from each other by clearing for a distance downstream from the source of the Abeba and upstream from their junctions with the Konshisha.

Of the two rivers, the Abeba was chosen as the experimental river because of its more continuous vegetation and high fly population. The vegetation on this river is divided roughly into halves conveniently demarcated by the motor-track crossing. That of the eastern or upper end is notable for its continuous, wide, thick growth, consisting dominantly of *Vitex cienkowskii*, *Syzygium guineense*, *Uapaca* spp., *Phoenix reclinata*, *Khaya senegalensis*, *Adina microcephala*, *Sterculia* spp., etc., forming a fairly continuous canopy beneath which lies a dense thicket of bushes and creepers varying from 5 to 40 yd. wide on either bank. Downstream of the track the vegetation is somewhat less dense, averaging between 5 and 10 yd. in width on either bank (see Pl. XV, fig. 2). On the whole this is confined to a narrow strip along the river, except at its junction with the River Amelungu where extensive thick woodland adjoins the river on either side. The total length of the Abeba isolated for spraying, together with its seven tributaries, was $8\frac{1}{4}$ miles. All the tributaries have sparse vegetation except for the River Ukwen, which supports vegetation even heavier than the heavier parts on the Abeba, never becoming less than 25 yd. wide on either bank (see Pl. XV, fig. 1). The control river (the Avende) supports a low fly population, the reason for which is unknown, and apart from a stretch almost devoid of vegetation for half a mile on either side of the motor-track crossing, has dense growth along its entire length.

Both rivers contain flowing water throughout the year.

Description of Fly-rounds.

With the staff available, and considering the length of time over which the rounds would have to be maintained, it was decided that as simple a form of fly-round as possible would be advisable. A stretch of river, $\frac{3}{4}$-mile in length, was therefore chosen on each river, each stretch being divided into six sections of 130 yd. each. The method used was that one Tsetse Control Assistant (fly-boy) with a labourer to act as bait would remain in each section for one hour each day, recording species and sex of, and retaining, all flies caught, releasing them at the end of the hour, and then moving on to the next section. As the initial fly population was low, all flies had thus been released at the end of the day to avoid depleting the population by catching out. The positions of these two fly-rounds, with sections numbered 1–6, are indicated in fig. 2. All fly-rounds were started at 10 a.m.

These stretches of river formed the main fly-rounds. In addition to them, six check points were set up in likely places such as cattle crossings, washing places, etc., along the Abeba. These are indicated by the letters A–F on the Abeba only. At these points, catchers remained stationary for half an hour at each point. At a later date, after the first year's spraying, a further four points were also selected on the Ukwen. Two catchers remained stationary for an hour at each of these points. Three further sections, numbered 7 to 9, were set up later on the Avende.

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* The current clearing technique used by the Sleeping Sickness Service in this province is that of Partial Clearing as described by Nash (1940).

In this type of clearing only the low shade is removed while the majority of the tall emergents (such as mahogany) are left standing. This is only intended to be unsuitable for fly during the dry season, and therefore, at the end of each season's work, a Ruthless Barrier is cut to prevent reinvasion. This type of clearing has been found to be very successful, and in all about 200 sq. miles of land in the region of the experiment have been freed from fly by this means.

Method of Spraying.

After one or two trials, the following technique was decided upon as being the most effective. Using the four Eclipse Warley knapsack pressure sprayers available, the labour force was divided into two teams, each consisting of two men to apply the spray, two carriers, and one mixer, all five being supervised by a Tsetse Control Assistant whose main job was to make sure that the spray was applied to the correct places, *e.g.*, the underside of overhanging vegetation and the trunks of trees and branches within 6 ft. of the ground. Roots projecting from steep banks were also treated.

The DDT was carried in its concentrated form to the river, where it was mixed in a large drum with river water, usually in 20-gallon batches. The carriers then kept pace with the spraying, replenishing the machines when necessary.

For the first two applications in 1955, 50 per cent. paste was used, but was later discontinued owing to the difficulty in mixing, and also because the tins tended to become damaged by rough handling so that the liquid wetting agent leaked away. For all subsequent applications 50 per cent. wettable powder was used.

It was originally intended to use a 5 per cent. suspension for all applications but, owing to curtailments of supplies and delays in delivery, 2½ per cent. was used on many occasions. It was considered that this would not cause too adverse an effect as in any case the operators showed a tendency to apply too much insecticide unless supervision was very strict.

TABLE I.

Details of application of DDT.

Application no.	Date	Preparation	Concentration of DDT %	Rate of application (lb. 50% product/mile)	Remarks on extent of application
1	24 Jan.–1 Feb. 1955	Paste	5	22·7	Vegetation on river banks only
2	2–22 Mar. 1955	Paste	2½	42·6	All vegetation to 20 yd. from bank
3	2–12 May 1955	W. powder	2½	21·3	As for 1st application
4	5–13 Dec. 1955	W. powder	5	72·7	Liberally to 10 yd. from bank
5	22–27 Dec. 1955	W. powder	2½	26·3	Vegetation on river banks only
6	5–14 Jan. 1956	W. powder	2½	37·3	do.
7	19 Jan.–3 Feb. 1956	W. powder	2½	40·2	do.
8	7–21 Mar. 1956	W. powder	5	54·5	Selected sites only

As the first application, limited to vegetation on the river banks, did not achieve a complete kill, and toxicity tests indicated a persistence of only 28 days, it was decided that the second application should be made to everything within 20 yd. of the river bank. Shortage of stocks of DDT dictated that the spray should be applied as a 2½ per cent. suspension to this greatly increased area. The spraying itself presented considerable difficulties in the thicker vegetation (see Pl. XV, fig. 1). Consequently on the Ukwen a path was cut straight through the middle of the forest regardless of the course of the river. It was hoped that

this would have a two-fold effect. It would enable the operators to penetrate the vegetation and would form a flight line (Nash & Page, 1953, p. 167) along which it was hoped the fly might congregate.

It will be noted from figs. 3 & 4 that the first three applications did reduce the fly population somewhat, but as they were undertaken at a time when the average daily catch for the month on the control river was on the decrease the effect of the DDT is difficult to estimate.

Following the lessons learnt during the first year's work it was decided that the next treatment should consist of four applications at fortnightly intervals covering a minimum effective period of eight weeks, about double the pupal incubation period at that time of year. Spraying also was to start in early December when the average daily catch of fly was expected to be on the increase. The first application of that season was of 5 per cent. suspension but owing to curtailment of supplies subsequent treatments had to be of $2\frac{1}{2}$ per cent. suspension. For this reason, and because there were still flies to be found on the river, a last and fifth treatment, of 5 per cent. DDT, was undertaken in March, spraying being confined to selected sites such as washing places, crossings, etc. In addition the whole of the Avende east of the motor track was cleared during October 1955 to reduce the possibility of reinvasion of the Abeba from the control river. To replace the three fly patrol sections thus destroyed, three similar sections, numbered 7 to 9 (see fig. 2), were set up on the western part of the river.

Toxicity of Deposits.

Tests were carried out after the first application, and deposits were found to be toxic to *G. palpalis*, after 30 seconds' contact, for a period of up to 28 days after spraying. After this period the deposit was found to be unreliable, kills being obtained in some instances and not in others. The method used was as follows. Flies were caught on another river and immediately placed in tubes. When sufficient had been caught they were fed and then placed individually on treated leaves until they had been in contact with the leaf for about 30 seconds. They were then kept under observation, and the lapse of time before signs of distress, knockdown, and death occurred was noted.

Unfortunately, it was not possible to undertake these tests on a large scale because undamaged flies were hard to collect in sufficient numbers.

A factor which was found to have an influence of considerable importance on the effective area of foliage bearing a toxic deposit (this is assuming that leaves are important as a resting site for tsetse) was the remarkable rate of growth of new foliage during the three weeks or so preceding the onset of the rains. One small tree trebled the number of its leaves in two weeks, thereby reducing the effective sprayed area by two thirds. For this reason alone it is of great importance to know the exact resting sites used by tsetse, information about which is very limited at present.

Effect on Fly Population.

The average numbers of flies of each species caught per visit over each month on each river are shown in figs. 3 and 4. As already described the two initial fly patrols (on fly-round and check points, respectively) on the Abeba were later increased, by the addition of a further group of check points, to three, all operating at the same time. The results have been adjusted to allow for this. The same number of catchers took part in all fly patrols.

The catches of *G. palpalis* (fig. 3) and of *G. tachinoides* (fig. 4) are best considered separately.

There is little doubt that the spraying in 1955 did have some considerable effect in reducing the population of *G. palpalis*, but was not quite efficient enough

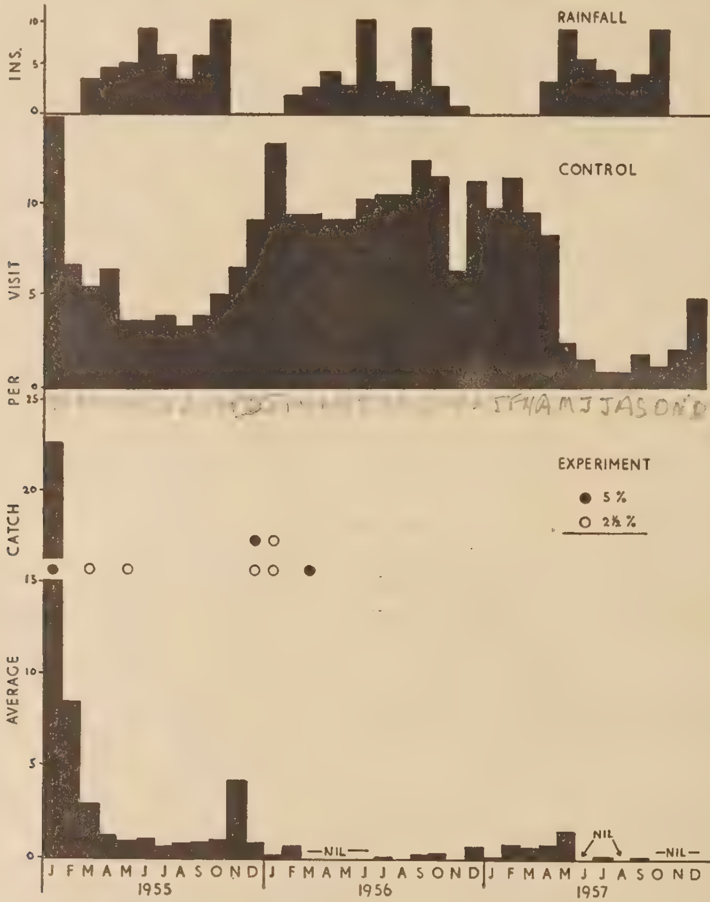

Fig. 3.—Histograms showing the average numbers of examples of *G. palpalis*, both male and female, caught per visit to the control and experimental rivers during each month. Spraying is indicated by a circle, the $2\frac{1}{2}$ per cent. suspension by an open circle, the 5 per cent. suspension by a closed circle. Monthly rainfall is also shown.

to eliminate them all. The actual efficiency is difficult to estimate as spraying took place at a time when the population on the control river was on the decline. For this reason the spraying in the second season was arranged so as to take place in December and January at a time when the population was expected to be on the increase, and, as can be seen from fig. 3, was, with the addition of a partial application in March, wholly successful, resulting in complete elimination of fly for a period of 124 days (almost 18 weeks). No flies were caught anywhere on the Abeba between 23rd February and 29th June 1956 (included in the July catch in fig. 3), when one male of *G. palpalis* was caught at a washing place in section 1. From September onward there has been found present a small

population which now appears to be on the increase, though for some reason no example of this species was caught during September to December 1957.

Gboko is situated almost at the southern limit of the range of *G. tachinoides* so it is therefore to be expected that its behaviour may not run entirely true to

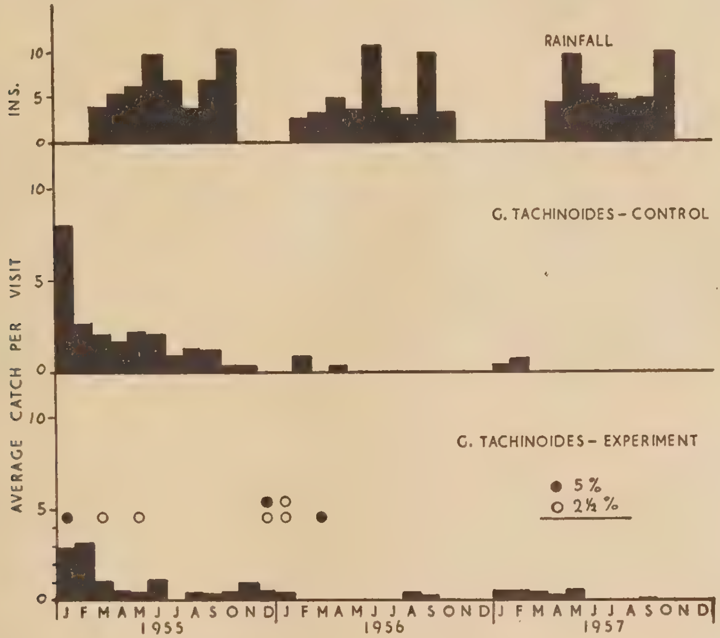

Fig. 4.—Histograms showing the average numbers of examples of *G. tachinoides*, both male and female, caught per visit to the control and experimental rivers during each month. Spraying is indicated by a circle, the 2½ per cent. suspension by an open circle, the 5 per cent. suspension by a closed circle. Monthly rainfall is also shown.

pattern. Indeed the suspicion that *tachinoides* is only confined to the riverine vegetation in this area in the height of the dry season is substantiated by the catches on the control river.

The average daily catch of *G. tachinoides* along the rivers (fig. 4) shows a peculiar feature on the control river in that the drop in catch there, which coincided with the first application of insecticide to the experimental river and had its counterpart in the catch of *G. palpalis*, showed no sign of recovery from September 1955 onward as it did in the case of *G. palpalis*, and no flies were caught there in December and January. There was therefore little against which the decline on the experimental river could be compared.

The second season's spraying appeared to eliminate *G. tachinoides* from the Abeba for six months, the only flies caught after that being in August and September at two cattle crossings at points A and E, suggesting that the flies may have been attracted by a herd of cattle which had moved into the area between the two rivers during that year. The catch on the control river continued to decline during 1956 and no flies were caught between the end of April and the end of December. It is thought that the clearing of the whole of the Avende east of the motor track in October (see p. 431) might have accounted for this continued decline in catch on the control river. It seems likely that, with a species such as *G. tachinoides*, clearing a river affects not only the population on

that river but also the population in the area as a whole, by reducing the number of possible habitats to which the fly can return during the dry season. In 1957, *G. tachinoides* reappeared on the control river in January and February but was absent thereafter. On the experimental river it was present up till the end of May, reappearing in September only. Observations were concluded at the end of the first week of December.

Cost.

The absolute cost of such an undertaking is always hard to estimate, but excluding the initial outlay required in purchasing sprayers and also excluding the salaries of the senior staff involved, the total cost of the first three applications was almost £154, or about £18 10s. per mile. In the 1956 series, when the rate of application was heavier, the total cost of the five applications was £416, or £50 10s. per mile. Partial clearing by paid labour on this river would have cost in the region of £100 per mile, so spraying represented in 1956 a saving of half the cost of partial clearing. It is admitted that the spraying was not in the long run completely successful, whereas partial clearing would have been. It should be pointed out, however, that for partial clearing to be effective the new undergrowth must be reslashed at least once a year, at additional cost. Otherwise it will rapidly become habitable for any tsetse flies that may reinvade the river.

Conclusions.

The trial can be deemed a success in that the fly population was reduced to zero which, in the case of *G. palpalis*, can be attributed to the spraying. That this absence of fly only lasted 18 weeks was unfortunate, but the period is considered too long for a small population to have existed undetected, and has led to the belief that free ranging between rivers during the rainy season may extend further than was originally supposed. Further work is now being undertaken to investigate this possibility. It is not possible to attribute the decline and temporary disappearance of *G. tachinoides* to the insecticidal treatment because a similar decline and disappearance took place on the control river at the same time.

The period of effectiveness of the deposit seems to be much shorter in this area than in the northern part of the country where similar tests to those described showed deposits to be toxic after 2½ months. This could possibly be due to reduction in availability of DDT to flies in humid conditions (Barlow & Hadaway, 1952, p. 98).

As a result of experience gained, it is concluded that spraying would be an ideal method of control in this heavy type of vegetation, provided isolation can be made complete. Since this trial took place, an isolated town with neighbouring banana and oil-palm plantations was treated in a similar manner, in January 1957, and elimination so far has been complete.

It is intended to undertake a further trial using dieldrin on the same river in an attempt to get a longer persistance. In order to eliminate the possibility of reinfestation of the Abeba from the Avende, both rivers will be treated, another river being chosen as a control.

Comments on Fly Population.

As this appears to be the first instance in which any continuous record of fly population has been kept in this area of West Africa, it is felt that some comment on the seasonal variation of population would not be out of place. In this respect it is unfortunate that the records were kept for reference in a field trial with insecticides and not for an ecological study, with the result that there

is no record of evaporation rates or humidities on the rivers. The rainfall figures were obtained from an Agricultural Station some 13 miles away.

With regard to the variations in the catch of *G. palpalis* on the control river it will be noted, if 1956 is omitted, that there is a definite peak in December and January (dry season) falling quickly at first to a more gradual fall off with a minimum in August (wet season). This is the inverse of the findings made by Nash & Page (1953, pp. 99–103) 3° of latitude farther north, where the wet season, April to September, was the period of increase and the dry season, October to March, the period of decrease in population. They did observe, however, that there was a tendency for a small rise in population in December, which they attributed to the arrival of stranger tsetse forced in to the river under observation by desiccation elsewhere.

It has been thought for some time that the wet-season dispersal of *G. palpalis* away from the rivers may be greater than at first supposed. There is no definite proof of this, as casual attempts to catch tsetse away from the rivers, whilst not unsuccessful, have not produced sufficient flies to be significant. It is thought possible, however, that conditions during the rainy season may be such that the flies tend to be dispersed, thereby reducing the concentration at any particular point, and that, due to drier conditions elsewhere during the dry season, from December to February, the flies would be concentrated along the rivers, where they would be protected from the hot, dry Harmattan wind.

It also seems possible that rainfall in excess of about four in. per month might have some adverse effect on the population. This is substantiated by the fact that when the rains were prolonged and slight in 1956 the average monthly catch remained almost constant throughout the year, whereas in the other two years, when the rainfall in most of the wet-season months exceeded four in., the typical wet-season decline in average monthly catch was obtained. This constant level of average monthly catch in 1956 was not restricted to the Avende alone, as similar catches were obtained on another river in the area.

It seems, therefore, that the early and middle dry season (October to January) is the period of optimum conditions leading to increasing population. This is followed by a sharp drop in February at a period when the dry season becomes too severe and this is quickly followed by the first rains in March, which produce a further drop by the flooding of pupal sites and the dispersion of the flies. The population then remains at a minimum until the end of the rainy season in October when optimum conditions return and the population rises.

With regard to the fluctuations in the population of *G. tachinoides* it can only be pointed out that the area is almost on the southern limit of the range of this species and that conditions must be very critical. It is strange, however, that in the dry year of 1956 when *G. tachinoides* could have been expected to thrive, it was almost completely absent. It may be that the clearing of the eastern part of the Avende in October 1955 is in some way responsible for this.

Summary.

During 1955 and 1956 two attempts were made to eradicate *Glossina palpalis* (R.-D.) and *G. tachinoides* Westw. from 8¼ miles of heavily forested perennial river in Benue Province of the Northern Region of Nigeria by using DDT.

Descriptions of the rivers and the means employed in applying the DDT using knapsack sprayers are given, together with the effect of the insecticide on the fly population.

It was found that it was possible to eliminate *G. palpalis* from this type of habitat, where the forest is largely restricted to the immediate vicinity of the rivers, but that isolation must be carefully undertaken to prevent reinvasion, which would appear to be more extensive than had been expected. *G. palpalis* was completely absent for 18 weeks.

G. tachinoides, which was present in much smaller numbers, also disappeared on the treated river, but because of a similar disappearance on the control river it is not possible to attribute this to the insecticidal treatment.

The cost of spraying was about half the cost of clearing by normal current methods.

Acknowledgements.

The author wishes to express his gratitude to the Director of Medical Services, Northern Region, Nigeria, for permission to publish this paper, and to Mr. R. J. Kernaghan, Senior Entomologist, Sleeping Sickness Service, under whose direction the experiment was carried out. Thanks are also due to Mr. R. G. S. Crawford, Sleeping Sickness Control Officer, for his valuable advice and assistance regarding the many practical difficulties and the employment and supervision of labour; and also to the junior staff concerned for their industry in carrying out the tedious fly-rounds, year after year.

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FIG. 1. Spraying in thick forest on River Ukwen.

FIG. 2. Normal, more open river. Labourers spraying from river-bed outwards towards the bank.

THE PRODUCTIVITY OF VARIOUS MOSQUITO BREEDING PLACES IN THE SWAMPS OF UGANDA.

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Very little is known about what distinguishes the different types of the swamp habitat in Uganda, with respect to the breeding of mosquitos. For example, although neither *Anopheles gambiae* Giles nor *A. funestus* Giles, the principal vectors of malaria in most parts of Uganda, normally breeds intensively in the swamps, there is usually a zone at the land edge where a considerable amount of breeding of both species takes place (Hopkins, 1940). But *A. gambiae* disappears immediately one enters the papyrus (*Cyperus papyrus*) zone and *A. funestus* only extends into it for a very short distance; the middle of the swamp does not provide breeding facilities for either of these species (Hopkins, *op. cit.*).

Hancock (1934) showed that Namanve Swamp, on the shores of Lake Victoria, contained a considerable mosquito fauna, which varied according to the habitats provided by the different nature of the various parts of the swamp and by the work of reclamation. He studied some nine different types of pool (classified by the kind of habitat in which they were found) and observed that some species, *e.g.*, *Anopheles coustani* Lav., occurred in all, but abundantly only in one or two of the habitats. Other species, *e.g.*, *Culex univittatus* Theo. and *C. rubinotus* Theo., occurred in most but not all types of pool and, again, showed a marked preference for certain habitats. Still other species, *e.g.*, *C. duttoni* Theo. and *Ficalbia uniformis* (Theo.), were extremely selective, occurring exclusively in particular habitats. Namanve Swamp was almost entirely innocuous, from a malariological point of view, and the conditions suitable for *A. gambiae* appeared only when reclamation began.

Steyn (1946) found very large specific differences in the output of Anophelines in cultivated and uncultivated high-altitude swamps in Kigezi District. *Anopheles marshalli gibbinsi* Evans decreased greatly in cultivated swamps, while *A. christyi* (Newst. & Cart.) increased. *A. christyi* bred very extensively in cultivated swamps, but generally disappeared when neglected areas reverted to swamp. In untouched swamps, individual breeding places which were previously negative for this species produced it subsequent to cultivation. It bred where papyrus had been cut down, but tended to disappear as the papyrus regenerated. *A. coustani* also occurred more frequently in cultivated than in uncultivated swamps. Steyn concluded that the net result of cultivation of swamps was a very great increase in the amount of open water available for the breeding of Anophelines, which led to a much increased incidence of malaria in the district.

In the Sudan, Lewis (1948) found that, in the main swamps of the Jebel Aulia reservoir on the White Nile, the breeding conditions are determined by the prevalence of various aquatic and semi-aquatic plants, which affect mosquitos in different ways. As in Uganda, *A. gambiae* does not normally breed in the swamps away from the margins where it occurs chiefly in disturbed vegetation. In the Kosti swamps, there was generally a preference by both Culicine and

Anopheline mosquitos for breeding in the patches of submerged plants and damaged (trodden, recumbent and semi-recumbent) sedge.

Reid (1953) states that, in South-East Asia, all members of the *Anopheles hyrcanus* (Pall.) group are typically swamp breeders, but that individual species within the group show important differences in their larval ecology. He points out that *A. nigerrimus* Giles seems to prefer deep swamps and swampy rice-fields in which the water surface is largely covered by plants, while a number of other species of the group seem to prefer shaded swampy situations, though not jungle swamp, and *A. sinensis* Wied. commonly breeds in sunlit waters.

The present observations form part of the work on the effects of man's interference on the mosquito fauna of swamps. The observations were undertaken to show the productivity of a number of selected types of the swamp habitat. Although *A. gambiae* was never found in any of the breeding places described in this paper, it is one of the long-term objectives of these investigations to discover the factors which inhibit the breeding of this species in swamps.

The observations were confined to two papyrus swamps only:—(1) Bukasa Swamp, on the shores of Lake Victoria, situated between Port Bell and Bukasa Forest, and west of Namanve Swamp, and (2) Lubigi Swamp, near Kampala, about six miles along the Kampala-Fort Portal road. Six different types of habitat were selected and classified very largely according to the recent history and condition of the papyrus as follows:—The papyrus, (I) cut freshly or recently; (II) burnt freshly or recently; (III) cut a long time previously; (IV) burnt a long time previously; (V) virgin or completely regenerated. Type VI consisted of the periphery of swamps with permanent and semi-permanent pools.

Types I and II were to be found for a period of up to about eight weeks from the time of cutting or burning, respectively, of the papyrus. The lengths of time after cutting or burning at which Types III and IV were to be found, and for which they persisted, were rather variable, but were generally about ten weeks, and up to some four or five months, respectively, from the time of these human activities. By the end of this period the papyrus had reached about half its original height.

Methods.

To obtain quantitative data, a "sampler" was employed. This was a wooden framework in the shape of a box, of internal dimensions 41 × 40 cm. by 18 cm. deep, open at both the top and bottom. It was placed in the area to be sampled, as quickly as possible, in order to avoid frightening the larvae away. In shallow water the sampler could be firmly fixed in place by means of prongs at the four corners of the bottom edges; in very deep water it was simply floated. In either case, the same amount of surface—an area of 1,640 sq. cm.—could be sampled. The surface water enclosed within the sample was carefully baled into a standard bucket, by means of an enamel bowl, at intervals of about one or two minutes. Two such bucketfuls constituted a sample. All mosquito larvae in the sample were then separated from the water, sorted out and counted. In each type of habitat 25 collections were made, thus making 150 samples altogether. The method is, however, quite unsuitable for larvae of certain species, *e.g.*, those of the genus *Taeniorhynchus*, which obtain air by piercing the roots or stems of submerged plants and do not come to the surface to breathe. Such species were therefore excluded from the present study, and any conclusions arrived at are restricted to that extent.

A number of chemical analyses of the water from the six types of habitat was made. Six factors were investigated, *viz.*: pH, potassium, sodium, oxygen absorbed from permanganate, free and saline ammonia and albuminoid ammonia. The pH was measured with a glass electrode. K and Na were determined by the

Eel Flame Photometer. Oxygen absorbed was estimated by reduction of N/80 acid $KMnO_4$ in four hours at 27°C. Free and saline ammonia was determined by distillation into boric acid and titration; albuminoid ammonia was similarly estimated after oxidation by $KMnO_4$.

The observations were made between 17th January and 10th April 1957. This was within the period when there is extensive cutting and burning of papyrus by the local people and when one is likely to find all the habitats described existing simultaneously, thus permitting a fair comparative study. Only larvae were studied.

Results.

The distribution of the larvae of, altogether, 17 species of swamp-breeding mosquitos was studied. The species were *Anopheles coustani* Lav., *A. funestus* Giles, *Culex* (*Culex*) *annulioris* Theo., *C.* (*C.*) *decens* Theo., *C.* (*C.*) *grahami* Theo., *C.* (*C.*) *guiarti* Blanch., *C.* (*C.*) *univittatus* Theo., *C.* (*Neoculex*) *rubinotus* Theo., *C.* (*Lutzia*) *tigripes* Grp., *Ficalbia* (*Etorleptiomyia*) *mediolineata* (Theo.), *F.* (*Ficalbia*) *malfeyti* (Newst.), *F.* (*Mimomyia*) *hispida* (Theo.), *F.* (*M.*) *plumosa* (Theo.), *Hodgesia cyptopus* Theo., *Uranotaenia balfouri* Theo., *U. mashonaensis* Theo., and *U. pallidocephala* Theo.

The total number of larvae of all the 17 species collected from all the six types of habitat was 5,781. Details of the numbers of each species in this total and their distribution are shown in Table I. A study of this Table reveals that *Culex guiarti*, *C. univittatus* and *C. rubinotus* were the dominant species, comprising 32·8, 21·1 and 24·1 per cent., respectively, *i.e.*, altogether making 78 per cent. of the total number of larvae studied. None of the other 14 species singly exceeded 7·2 per cent. and most of them were much less numerous than this.

Taking the percentage of the total that is represented by the larvae collected from a type of habitat as a measure of the total productivity of that type, Table I reveals that, during the period covered by the present observations, Type VI (periphery of the swamps, with permanent and semi-permanent pools) was the most productive, with 49·9 per cent. of the total. The least productive were the habitats with burnt papyrus, *i.e.*, Types II (recently burnt) and IV (burnt a long time previously).

The distribution of individual species of mosquitos in the different types of the swamp habitat is also shown in Table I. It will be seen that out of the 17 species from the various habitats, only one (*C. tigripes*) was found in all the six types, while four (*A. funestus*, *C. grahami*, *C. guiarti* and *F. malfeyti*) occurred in Type VI only, and two (*F. mediolineata* and *F. plumosa*) in Type I only (recently cut). Three species (*C. annulioris*, *C. decens* and *F. hispida*) were found in three types, three (*C. univittatus*, *H. cyptopus* and *U. balfouri*) in four types, and four (*A. coustani*, *C. rubinotus*, *U. mashonaensis* and *U. pallidocephala*) in five types.

Some of the species were found fairly regularly in all the habitats in which they were recorded, *e.g.*, *U. pallidocephala*, whereas others were regular inhabitants of only certain of these habitats, *e.g.*, *A. coustani*, *C. univittatus* and *C. rubinotus*. Still other species were sporadic in all the habitats in which they were present, *e.g.*, *C. annulioris*, *H. cyptopus*, *U. balfouri* and *U. mashonaensis*. This is clearly shown, in Table II, by the number of occasions (out of a possible maximum of 25) on which the larvae of the different species were present in each of the various habitats.

TABLE I.

Details of the numbers and distribution of individual species, and total productivity of the various types of habitat.

Species	Number and percentage of larvae collected in each type of habitat												Total of each species	
	I		II		III		IV		V		VI			
	Number	%	Number	%	Number	%	Number	%	Number	%	Number	%	Number	%
A. coustani	0	0	4	2·3	1	0·6	10	5·8	27	15·8	129	75·5	171	3·0
A. funestus	0	0	0	0	0	0	0	0	0	0	8	100	8	0·1
C. annulioris	0	0	0	0	0	0	5	10·4	13	27·1	30	62·5	48	0·8
C. decens	2	1·1	0	0	0	0	1	0·6	0	0	176	98·3	179	3·1
C. grahami	0	0	0	0	0	0	0	0	0	0	32	100	32	0·6
C. guiarti	0	0	0	0	0	0	0	0	0	0	1893	100	1893	32·8
C. univittatus	601	49·3	36	3·0	0	0	5	0·4	0	0	577	47·4	1219	21·1
C. rubinotus	490	35·2	47	3·4	448	32·2	33	2·4	374	26·9	0	0	1392	24·1
C. tigripes	2	3·5	29	50·9	4	7·0	10	17·5	11	19·3	1	1·8	57	1·0
F. mediolineata	16	100	0	0	0	0	0	0	0	0	0	0	16	0·3
F. malfeyti	0	0	0	0	0	0	0	0	0	0	42	100	42	0·7
hispida	48	60·8	0	0	19	24·1	0	0	12	15·2	0	0	79	1·4
F. plumosa	5	100	0	0	0	0	0	0	0	0	0	0	5	0·1
H. cyptopus	2	8	7	28	11	44	0	0	5	20	0	0	25	0·4
U. balfouri	4	3·3	3	2·5	24	20	0	0	89	74·2	0	0	120	2·1
U. mashonaensis ..	7	9·2	3	3·9	16	21·1	8	10·5	42	55·3	0	0	76	1·3
U. pallidocephala ..	73	17·4	25	6·0	125	29·8	82	19·6	114	27·2	0	0	419	7·2
Total of all species ..	1250	21·6	154	2·7	648	11·2	154	2·7	687	11·9	2888	49·9	5781	100

Omitting those species that occurred exclusively in a particular habitat (*A. funestus*, *C. grahami*, *C. guiarti*, *F. mediolineata*, *F. malfeyti* and *F. plumosa*) and on the basis of total numbers of larvae, the following breeding preferences were shown by the various species (see Table I):—Type I (freshly or recently cut papyrus areas) was preferred by *C. univittatus*, *C. rubinotus* and *F. hispida*; Type II (freshly or recently burnt papyrus areas) by *C. tigripes*; Type III (long-standing cut papyrus areas) by *H. cyptopus* and *U. pallidocephala*; Type V (virgin or completely regenerated papyrus areas) by *U. balfouri* and *U. mashonaensis* and Type VI (periphery of swamps with permanent and semi-permanent pools) by *A. coustani*, *C. annulioris* and *C. decens*. None of the species showed any particular preference for Type IV (long-standing burnt papyrus areas).

TABLE II.

Frequency of larval occurrence.

Species	Number of times larvae were present in type of habitat						Total larval occurrence
	I	II	III	IV	V	VI	
A. coustani	0	3	1	4	6	19	33
A. funestus	0	0	0	0	0	3	3
C. annulioris	0	0	0	1	1	5	7
C. decens	1	0	0	1	0	11	13
C. grahami	0	0	0	0	0	7	7
C. guiarti	0	0	0	0	0	20	20
C. univittatus	8	5	0	2	0	20	35
C. rubinotus	20	8	21	9	22	0	80
C. tigripes	2	13	3	7	4	1	30
F. mediolineata	4	0	0	0	0	0	4
F. malfeyti	0	0	0	0	0	14	14
F. hispida	11	0	8	0	5	0	24
F. plumosa	1	0	0	0	0	0	1
H. cyptopus	2	3	3	0	3	0	11
U. balfouri	2	4	7	0	8	0	21
U. mashonaensis ..	3	2	4	5	4	0	18
U. pallidocephala ..	17	12	15	18	19	0	81

As regards the number of species found in each type of habitat, all six produced about equal numbers, as shown in Table III. This Table also shows the degree of resemblance between habitats, according to the extent to which they harbour the same species. It will be seen that Type VI had no very close faunistic similarities to any of the other five types; but it was closest to Type IV. Types I, II, III, IV and V shared many species in various combinations.

TABLE III.

" Species Production " and resemblances between habitats.

Type of habitat	Total number of species collected in type	Number of same species also collected in type					
		I	II	III	IV	V	VI
I	11	—	7	7	6	7	3
II	8	7	—	7	6	7	3
III	8	7	7	—	5	8	2
IV	8	6	6	5	—	6	5
V	9	7	7	8	6	—	3
VI	9	3	3	2	5	3	—

TABLE IV.

Association of species (figures in columns represent the number of times a species was found together with another).

Species	*A. coustani*	*A. funestus*	*C. annulioris*	*C. decens*	*C. grahami*	*C. guiarti*	*C. univittatus*	*C. rubinotus*	*C. tigripes*	*F. mediolineata*	*F. malfeyti*	*F. hispida*	*F. plumosa*	*H. cyptopus*	*U. balfouri*	*U. mashonaensis*	*U. pallidocephala*
A. coustani ..	—	3	3	9	4	14	17	9	6	0	9	1	0	0	0	2	6
A. funestus ..	3	—	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0
C. annulioris ..	3	0	—	1	1	5	2	1	0	0	5	0	0	0	1	1	1
C. decens	9	0	1	—	3	8	10	2	1	1	8	0	0	0	0	0	0
C. grahami ..	4	0	1	3	—	6	4	0	0	0	5	0	0	0	0	0	0
C. guiarti ..	14	2	5	8	6	—	14	1	1	0	12	0	0	0	0	0	0
C. univittatus ..	17	2	2	10	4	14	—	5	3	3	12	2	0	0	0	1	5
C. rubinotus ..	9	0	1	2	0	1	5	—	13	2	0	20	1	9	16	14	45
C. tigripes ..	6	0	0	1	0	1	3	13	—	0	1	4	0	2	3	3	16
F. mediolineata ..	0	0	0	1	0	0	3	2	0	—	0	1	0	0	1	0	1
F. malfeyti ..	9	0	5	8	5	12	12	0	1	0	—	0	0	0	0	0	0
F. hispida ..	1	0	0	0	0	0	2	20	4	1	0	—	1	4	7	7	18
F. plumosa ..	0	0	0	0	0	0	0	1	0	0	0	1	—	0	0	0	1
H. cyptopus ..	0	0	0	0	0	0	0	9	2	0	0	4	0	—	5	3	8
U. balfouri ..	0	0	1	0	0	0	0	16	3	1	0	7	0	5	—	4	16
U. mashonaensis ..	2	0	1	0	0	0	1	14	3	0	0	7	0	3	4	—	16
U. pallidocephala	6	0	1	0	0	0	5	45	16	1	0	18	1	8	16	16	—

The association of species—whether certain species occur singly or with others—is shown in Table IV. From this it will be seen that the various species showed different degrees of association. Of particular interest are species like *C. guiarti* and *F. malfeyti* which, although restricted to one type of habitat, were associated there with others that were more widespread.

Some of the results of the chemical analysis of water from the six types of habitat are shown in Table V. It will be seen that Type V (virgin or completely regenerated papyrus areas) contained the greatest amount of both K and Na. Also, habitats with recently cut papyrus (I) had less K and Na than those with recently burnt papyrus (II). But, while long-standing cut papyrus areas (III) had considerably less K than those with long-standing burnt papyrus (IV), there was very little difference in the amount of Na between Types III and IV. The least amount of both absorbed oxygen and albuminoid ammonia was found in the burnt papyrus habitats (II and IV). Free and saline ammonia was least in Type I (recently cut papyrus areas) and highest in VI (periphery of swamps). The pH was variable in all the six types and generally within the same broad limits.

Discussion and Conclusions.

The swamp environment is not a uniform one and it provides a considerable variety of conditions for the breeding of mosquitos. This is especially so when and where swamps have been altered by human interference, which takes various forms. For example, reclamation of swamps may involve afforestation, drainage, clearing and cultivation, while cutting and burning of papyrus and other swamp plants is a common practice. Some of the areas so altered may be abandoned, and revert to swamp.

As regards the breeding of mosquitos, it is sometimes possible to draw a sharp dividing line between the more productive and the less productive habitats. The results of the present study give sufficient evidence for the view that peripheral zones of swamps, especially if untouched, are much more productive than the interior. Of the six types of swamp habitat studied, it is shown that long-standing peripheral pools (Type VI) were the most productive.

In another (unpublished) study, it was repeatedly noticed that where two sites existed, sometimes quite close to one another, where papyrus had (1) been cut, and had (2) been burnt, habitats with burnt papyrus produced considerably fewer mosquito larvae than did those with cut papyrus, irrespective of the time that had elapsed since the cutting or burning. The present observations support this conclusion since they show that the two types of habitat with burnt papyrus (II and IV) had the same degree of larval abundance and were the least productive of all the habitats. On the other hand, the present work shows that in an area of freshly cut papyrus the larval population is twice as great as in virgin or completely regenerated papyrus. Thus, as the result of man's activities, the productivity of an area of swamp can be very much increased or decreased, according to the nature of the interference. Hancock (1934) and Steyn (1946) showed how man's alteration of swamps may aggravate the malaria situation.

There was considerable variation in the species and numbers of mosquito larvae found in the six types of habitat. Some species, *e.g.*, *C. tigripes*, were widely distributed, while others, *e.g.*, *C. guiarti*, were restricted to particular habitats. However, the six types produced about an equal number of species. The most abundant species were *C. guiarti*, *C. univittatus* and *C. rubinotus*.

Some of the species occurred in about equal total numbers in two or more types of habitat, but while they were always present in some habitats, they were rather sporadic in others. Thus, although two habitats may produce the same total number of larvae of a given species over a certain period, the numbers at any one time may not be the same in both. This serves to emphasise how figures based on single observations may give a false impression of the similarity or

TABLE V.

Results of the chemical analysis of water from the six types of habitat.
(All factors expressed in parts per million.)

Date	Habitat Type I						Habitat Type II					
	pH	K	Na	Absorbed O_2	F.S.A.	A.A.	pH	K	Na	Absorbed O_2	F.S.A.	A.A.
Feb. 11	7·6	20·0	13·0	0·00122	0·04	0·11	7·4	52·5	19·30	0·00066	0·04	0·11
Feb. 18	6·3	12·6	17·34	0·00158	0·28	1·55	7·5	46·6	15·37	0·00121	0·39	1·27
Feb. 25	7·0	14·2	12·61	0·00146	0·22	1·12	6·6	38·8	11·43	0·001	0·34	0·88
March 4	7·1	24·1	12·61	0·00225	0·24	1·91	7·1	24·1	12·61	0·00225	0·24	1·91
Average		17·7	13·89	0·00163	0·20	1·17		40·5	14·68	0·00128	0·25	1·04

Date	Habitat Type V						Habitat Type VI					
Feb. 19	7·5	12·6	16·83	0·00347	0·54	1·52	7·2	20·0	14·97	0·00242	0·45	1·55
March 5	7·4	127·1	17·73	0·00314	0·22	1·35	6·8	7·3	10·64	0·00138	0·30	0·78
March 26	6·6	45·1	16·15	0·00241	0·21	0·94	7·3	22·0	10·64	0·00277	0·34	2·43
April 10	7·4	43·0	14·58	0·00247	0·21	1·34	7·9	27·2	15·37	0·00191	0·43	1·38
Average		57·0	16·32	0·00287	0·30	1·30		19·1	12·91	0·00212	0·38	1·54

Date	Habitat Type III					
	pH	K	Na	Absorbed O_2	F.S.A.	A.A.
Feb. 11	7·8	16·2	16·94	0·00103	0·32	1·35
Feb. 25	7·1	14·2	11·43	0·00386	0·41	3·39
March 19	7·5	27·8	14·58	0·0022	0·22	1·08
April 1	6·7	32·5	13·00	0·00104	0·09	0·69
Average		22·7	13·99	0·00203	0·26	1·78

Date	Habitat Type IV					
	pH	K	Na	Absorbed O_2	F.S.A.	A.A.
March 19	7·4	45·1	13·00	0·00117	0·22	0·97
March 25	6·7	40·8	10·24	0·00036	0·22	1·00
April 1	6·5	29·3	15·76	0·00104	0·30	0·66
April 8	7·6	30·9	14·79	0·00247	0·21	1·37
Average		36·5	13·45	0·00126	0·24	1·00

F.S.A. = Free and Saline Ammonia; A.A. = Albuminoid Ammonia.

dissimilarity between habitats. The species may find breeding conditions in one place suitable over a very long period and production would be continuous and steady. But such favourable conditions may exist in the other place only occasionally and for short periods, reflected in a sporadic and explosive increase of larvae.

In comparing one habitat with another, attention should be paid to the pattern of species present, which is likely to be more significant than the number either of species or of individuals. Similarity of habits will bring about association of species, and species which have dissimilar habits will be expected to occur in different habitats (Russell & Rao, 1940). *C. rubinotus*, *F. hispida* and *U. pallidocephala* were "strongly" associated and were all abundant to a greater or less extent in Types I (papyrus, recently cut), III (papyrus, cut a long time previously) and V (papyrus, virgin or completely regenerated). But distinctions can be drawn between these three types of habitat on the same basis. Two of the three species (*C. rubinotus* and *F. hispida*) were, within the three habitats, most abundant in Type I and least in Type V, while *U. pallidocephala* was most abundant in Type III and least in I. The three types of habitat were therefore not equally favourable to all the three species.

Apart from *C. tigripes* (see below), only three species (*C. rubinotus*, *U. mashonaensis* and *U. pallidocephala*) were common to all the types I–V (but excluding VI) and, in respect of the other species, these five types of habitat differed much from each other, though Types III and V were most closely related. Type VI had no close similarities with any of the other five, but was closest to IV (papyrus burnt a long time previously).

Only one species, *Culex tigripes*, was found in all the six types of habitat. Since the breeding places of this species seem to be limited more by the presence or absence of other mosquito larvae on which to prey than by any other factor (Hopkins, 1952), the availability of suitable food in all the six types would explain its distribution. It is, however, interesting to note that *C. tigripes* was the most abundant in Type II (recently burnt papyrus), one of the two least productive types. At no time were larvae of other species found in any appreciable numbers in this type when *C. tigripes* was also present. This would suggest that this species was controlling the others and was responsible for the low productivity of Type II. It is not uncommon to find *C. tigripes* occurring in a habitat in which no other larvae are present, which suggests that under some circumstances its control of the other larvae is complete (Jackson, 1953).

The distribution of *C. annulioris* was probably governed by the presence of filamentous green algae. The usual breeding places of this species are characterised by clean water containing these algae, among which the larvae lurk (Hopkins, 1952), and in the writer's experience they are restricted to such waters.

Types I (papyrus recently cut), II (papyrus recently burnt) and VI (periphery of swamps) had one feature in common. They were all well exposed to sunlight, though in Type I the immediate water surface was more shaded than in the others, being covered with cut papyrus and other vegetation and, during flooding, it had much floating débris. It might be expected that a reduction in free water surface by floating débris would restrict mosquito breeding. This, however, is not borne out by these observations, since Type I with its reduced free water surface was actually more productive than II, which had been burnt and was relatively free of floating material. In fact, increasing the amount of open water by burning the papyrus proved unfavourable. Cutting and burning seem, therefore, to affect the breeding of mosquitos differently. These two processes presumably give rise to different changes in the physico-chemical or biological characters of the water.

The results of the chemical analysis of water show that the two most productive types of habitat (I—recently cut papyrus, and VI—periphery of swamps) contained a considerably smaller amount of potassium than the two least productive (II and IV—papyrus burnt recently and long previously, respectively). But,

since Type V (virgin or completely regenerated papyrus areas), which was more productive than either II or IV, contained the greatest amount of K, it cannot be concluded that the greater amount of the factor in II and IV (than in I and VI) was inhibitory to breeding. A similar but less marked trend is evident in concentrations of sodium, to which the same argument applies.

The pH in the six types varied within generally the same broad limits and does not seem to have been associated with the productivity of the different types.

The amount of free and saline ammonia was least in Type I and greatest in VI. Therefore, although this factor was highest in the most productive type (VI), it was least in the next most productive (I), which suggests that there was no relation between free and saline ammonia and productivity.

The amount of oxygen absorbed and the quantity of albuminoid ammonia are good indications of the amount of organic matter present. On this basis, the least productive habitats (II and IV—those which had been burnt) had the least amount of organic matter, and this suggests that there was a relation between soluble organic matter and productivity. But burning may affect the water in some other way and it is hoped to investigate this possibility.

Other possible factors in swamp water, which were not investigated, but which may have had some relation to the productivity of the various habitats, include (1) the nature of the soluble oxidisable organic matter, (2) conductivity, (3) ferruginous surface films and (4) iron in solution.

Soluble organic matter may be of animal or vegetable origin. Generally, peripheral zones of swamps (at least in Uganda) have more animal life—in the form of tadpoles, snails, various aquatic insects, Ostracoda, Cladocera, etc.—than the interior. As a result of death and decay of these animals, it would be expected that peripheral zones would have more organic matter of animal origin than the interior. On the other hand, the interior zones would presumably have more organic matter of vegetable origin than the peripheral.

Senior-White (1926) in Ceylon showed that the concentration of solutes in water, approximately indicated by electrical conductivity, was related to specific distribution of Anophelines. It would be worth investigating what differences there are between the various swamp habitats with respect to this factor and whether it bears any relation to productivity.

It is a common observation in the tropics that waters with ferruginous surface films are generally free from mosquito larvae (Williamson, 1944). This statement is, however, incorrect with respect to swamp waters (at least in Uganda). Mosquitos, especially Culicines, breed very intensively in swamp habitats containing rusty deposits or bearing iridescent ferruginous films. Another closely related factor is dissolved iron. Hancock (1930) suggested that the absence of Anopheline mosquitos might be correlated with a high concentration of dissolved iron salts. The concentration of iron was very low at Namanve Swamp, but it might be that in some swamps iron is present only where there is a high organic content in the water (Hancock, 1934).

Summary.

Six types of habitat in papyrus (*Cyperus papyrus*) swamps in Uganda were studied with regard to the production of mosquito larvae. A classification of the types is given, which was largely based on the lapse of time since temporary clearing by cutting or burning had been carried out.

Altogether a total of 5,781 larvae belonging to 17 species was studied. *Culex* (*Culex*) *guiarti* Blanch., *C.* (*C.*) *univittatus* Theo. and *C.* (*Neoculex*) *rubinotus* Theo. were the dominant species, comprising together 78 per cent. of the total number of larvae. *Anopheles gambiae* Giles was not recorded. Samples of larvae were taken at intervals between mid-January and early April 1957. The sampling method used was unsuitable for those species of which the larvae obtain air from

roots or stems of submerged vegetation, and these were excluded from the present study.

There was considerable variation in species and numbers of larvae and in their frequency in the different types of habitat.

It is concluded that (a) peripheral zones, especially in natural untouched swamps, are much more productive than the interior, (b) where swamps have been altered by cutting and by burning of papyrus and other vegetation, burnt habitats, whether recently or after the lapse of up to four or five months, have a very low productivity, (c) of the six chemical factors investigated (pH, K, Na, absorbed oxygen, free and saline ammonia and albuminoid ammonia) only the quantity of soluble organic matter, indicated by absorbed oxygen, and albuminoid ammonia, showed any relation to productivity, the least productive habitats containing the smallest quantity of organic matter.

Other possible factors in swamp water, which were not investigated, are mentioned. These are (a) the nature of soluble oxidisable organic matter, (b) conductivity, (c) ferruginous surface films and (d) iron in solution.

Acknowledgements.

This work was carried out under a scheme of research on tropical swamps supported by the Nuffield Foundation. I am very much indebted to Prof. L. C. Beadle, Director of the Scheme, for encouragement during the course of these observations and for discussion, reading and criticising the manuscript and advice in preparing this paper. I am also indebted to Mr. S. A. Visser, for the water analyses and discussion on the chemical aspects of the problem. I wish to thank Mrs. E. C. C. van Someren for kindly checking the identification of some of the species studied. Mention should also be made of the help received from my assistant, Mr. J. B. Nyangereka.

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OBSERVATIONS ON THE BIOLOGY OF *TROX PROCERUS* HAR. (COLEOPTERA, TROGIDAE), A PREDATOR OF EGGS OF THE DESERT LOCUST, *SCHISTOCERCA GREGARIA* (FORSK.).

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(Plate XVI.)

Four species of *Trox* have previously been recorded feeding on the eggs of locusts. In the Argentine, *Trox suberosus* F., known locally as " champi ", has for many years been recognised as a predator, in the larval and adult stages, on the eggs of *Schistocerca paranensis* (Burm.) (Conil, 1881; Bruner, 1898; Hayward, 1936). Bruner (1900) also stated that two other species of *Trox*, *T. aeger* Guér. and *T. pilularius* Germ., had been identified, but there was no indication as to whether these two species actually destroyed locust eggs.

In the Old World, three species of *Trox* have been recorded feeding on the eggs of the Desert Locust, *Schistocerca gregaria* (Forsk.). In 1942, Pruthi found larvae of *T. procerus* Har. in association with egg-pods of the Desert Locust in India, and suspected that they were feeding on the eggs (Gardner, 1947). In 1945 at Wardere, Somalia (now in Ethiopia), Hynes observed larvae of *T. procerus* feeding on the eggs of the Desert Locust (van Emden, 1948). Risbec (1946) found adults of what was probably *T. squalidus* Ol. (cited as *T. inaultus* Bdl., which is presumably an error for *T. incultus* Fhs., a synonym of *T. squalidus*) and *T. gemmatus* Ol. (cited as *T. gemmatus* F.) in 1944, destroying eggs of the Desert Locust at several localities in Senegal.

More recently, in the course of studies on egg-fields of the Desert Locust, *T. procerus* has been found on numerous occasions, and in the present paper an attempt is made to assemble all the information on the biology of this species.

Methods and Materials.

The observations recorded below were made by numerous workers in several countries, and in different circumstances, so that there was considerable variation in the methods of study used. Nevertheless, all the field data concerning the developmental stages were obtained during examinations of egg-fields of the Desert Locust.

The eggs of the Desert Locust are laid in the ground in pods which are, in general, invisible on the surface. Therefore, in order to study the eggs and associated predators and parasites, the egg-pods have first to be located in the soil. This may be done either by digging out the soil containing them or by removing a thin layer of soil above them to reveal the white froth-plugs which extend from the top of the egg-mass to the soil surface. The former method is frequently used by field workers as a crude but rapid way of ascertaining whether egg-pods are present in an area. The latter method enables the size of groups of egg-pods and the number and relative positions of them within groups to be assessed without disturbing them. A trench can then be dug to one side of a group of pods and by gradual removal of thin vertical slices of soil the depth of the egg-pods and the presence and the positions of predators can be determined. Further, the egg-pods and predators can be removed without damage for more detailed study. In this manner many of the observations on the biology

TABLE I.

Records of *Trox procerus* found in association with egg-fields of the Desert Locust.

Country	Locality	Lat. (°N.)	Long. (°E.)	Date of observation	No. *Trox procerus* found, and stage in life-cycle	Date of locust laying	No. days from locust laying to observation	Estimated egg mortality caused by *Trox*	Estimated egg mortality caused by agents other than *Trox*	Identification	Observer
India	Bharatpur	27 12	77 30	1942	Some larvae and one adult	Unknown	Unknown	Larvae suspected of feeding on eggs	Unknown	Adult identified as *Trox procerus* by J. C.M.Gardner (Gardner, 1947)	H. S. Pruthi
Saudi Arabia	Shaqqat-as-Shami	19 56	40 40	January 1953	Many larvae	*ca.* 15.i.1953	Larvae first observed about one week before hoppers hatched	Unknown but probably considerable	Unknown	Larvae stated by observer to be similar to those found by author in Saudi Arabia	C. E. S. Rennie
	9 miles south of Khumra	21 12	39 12	16.i.1956–10.ii.1956	Many hundreds of larvae; third instar more numerous than second	12–13.i.1956	10–25	*ca.* 30%, but see p. 463	Under 10%, but see p. 463	F. I. van Emden identified larvae as *T. procerus*	J. Roffey and R. A. Hall
	25 miles east of Lith	20 09	40 04	27.xii.1955	1 second- and 2 third-instar larvae	18–19.xii.1955	8–9	*ca.* 3%	*ca.* 6%		
	Shaqqat-as-Shami	19 57	40 40	31.xii.1955	A small number of larvae	18–19.xii.1955	12–13	*ca.* 20%	Unknown		
	Shaqqat-al-Yamani I	19 54	40 45	31.xii.1955	A small number of larvae	18–19.xii.1955	12–13	Considerable	Unknown		
	II			2.i.1956	2 larvae	18–19.xii.1955	14–15	*ca.* 75%	*ca.* 0·05%		
	6 miles north-west of Doga village I	19 42	40 52	30.xii.1955	Many second- and third-instar larvae	19–21.xii.1955	9–11	Considerable	Less than 1%		
	II			2.i.1956	3 larvae	19–21.xii.1955	12–14	*ca.* 15%	Less than 1%		
	9 miles north of Mozheilet	19 34	41 03	30.xii.1955	Small number of larvae	19–21.xii.1955	9–11	0%	0%		
	Between Wadis Yiba and Luma	19 24	41 14	31.xii.1955	Many larvae	19–21.xii.1955	10–12	Considerable	Small		
	2 miles south of Wadi Halatha	19 21	41 15	1.i.1956	Group (1) 11 larvae	19–20.xii.1955	12–13	97·21%	0·05%		
					Group (2) 24 larvae	19–20.xii.1955	12–13	87·59%	0·03%		
					Group (3) 3 larvae	19–20.xii.1955	12–13	*ca.* 80%	Unknown		

TABLE I.—*continued*.

Country	Locality	Lat. (°N.)	Long. (°E.)	Date of observation	No. *Trox procerus* found, and stage in life-cycle	Date of locust laying	No. days from locust laying to observation	Estimated egg mortality caused by *Trox*	Estimated egg mortality caused by agents other than *Trox*	Identification	Observer
Eritrea	Akbanazuf	15 55	39 07	21.i.1957	4 first-instar larvae	9.i.1957	12	0%	0%	Eggs at Shaba found in association with recently hatched first-instar larvae from which adult *T. procerus* were reared. Determined by E. B. Britton	D.J.Greathead
	Sheb I	15 54	39 03	15.i.1957	16 third-instar larvae	8.i.1957	7	2·5%	8·8%		
	II			19.i.1957	5 second- and 27 third-instar larvae	8.i.1957	11	10·0%	0%		
	Emberemi	15 46	39 23	February–March 1954	Adults common	25.ii.1954		0%	*ca.* 27%		
				8–12.xi.1956	Adults common	For several days		0%	29%		
	Ged-Ged	15 43	39 03	17.i.1957	1 egg, 1 first-4 second- and 1 third-instar larvae	5–7.i.1957	10–12	0·3%	*ca.* 9%		
	Shaba	15 39	39 03	9.i.1957	Eggs and 6 first-instar larvae	5–6.i.1957	3–4	0%	*ca.* 24%		
	Ailet I	15 33	39 09	December 1955	Adults common	26.xii.1955		0%	*ca.* 40%		
	II			12–14.i.1957	6 third-instar larvae	2–3.i.1957	9–12	0·5%	*ca.* 25%		
Ethiopia	Ado	7 19	45 10	24–25.xi.1953	Eggs, third-instar larvae and adults	Probably 19.xi.1953	5–6	*ca.* 0·6%	*ca.* 50%	Eggs found in association with adults in the ground; adults identified by R. D. Pope as *T. procerus*. Larvae identified by F. I. van Emden as *T. procerus*.	D. J. Greathead

TABLE I.—*continued.*

Country	Locality	Lat. (°N.)	Long. (°E.)	Date of observation	No. *Trox procerus* found, and stage in life-cycle	Date of locust laying	No. days from locust laying to observation	Estimated egg mortality caused by *Trox*	Estimated egg mortality caused by agents other than *Trox*	Identification	Observer
Ethiopia —*contd.*	Wal Wal	7 07	45 27	4.vi.1945	Larvae fairly common	24.v.1945	11	5·6%	86%	Adults reared from larvae were identified by G. J. Arrow as *T. procerus* (van Emden, 1948)	H. B. N. Hynes
	Wardere	6 57	45 25	3.vi.1945	Larvae common	*ca.* 22.v.1945	*ca.* 12	*ca.* 10%	*ca.* 1%		
	Ubatale	6 53	45 14	6.vi.1945	Larvae present	*ca.* 22.v.1945	*ca.* 15	Unknown	*ca.* 5% on 1.vi.1945		
	Afdub I	6 49	45 07	3.vi.1945	Few larvae	*ca.* 22.v.1945	*ca.* 12	Unknown	32–96%		
	II			6.vi.1945	Larvae present		*ca.* 15	Unknown			
	El Rago I	6 33	45 43	5–7.xi.1953	3 large larvae	25.x.1953	11–13	*ca.* 2%	*ca.* 50%	Similar to larvae found by author	P. E. Ellis
	II			11–12.xi.1953	1 large larva	31.x.1953	11–12	0·8%	*ca.* 30%		
	Scillave	6 25	44 42	October 1955	17 large larvae	*ca.* 20.x.1955	Larvae found 1–7 days before hoppers hatched	*ca.* 1%	*ca.* 50%	Similar to larvae found by author	P. E. Ellis
Somalia	Ferfer	5 05	45 07	3.xi.1952	Fairly common	*ca.* 25.x.1952	*ca.* 8	Unknown	Unknown	Larvae similar to those found at Hiran	P.R Stephenson
	Hiran	4 48	45 13	5.xi.1952	Small number of third-instar larvae	26.x.1952	9	Unknown	Unknown	Determined by F.I.van Emden as *T. procerus*	Z. Waloff
	Villagio	2 48	45 30	1945						Stated by observer to be similar to larvae found around Wardere	H. B. N. Hynes
Kenya	Korijub Moyale Dandu Takabba Bur Mayu El Wak Wajir	3 34 3 31 3 27 3 23 2 56 2 48 1 46	41 27 39 04 39 53 40 14 40 14 40 55 40 05	During incubation period of locust eggs	Large white grubs seen	*ca.* 21.xi.1955 24.x.1955 *ca.* 21.xi.1955 *ca.* 21.xi.1955 *ca.* 17.xi.1955 *ca.* 21.xi.1955 17.xi.1955	Unknown	Unknown but probably considerable	Heavy	Large white grubs are thought to be *Trox*	Locust Officers of Desert Locust Survey
	Wajir	1 46	40 05	December 1954	Adults common	13.xii.1954				Sight records of *Trox* species	D.J.Greathead

of *T. procerus* were made. In Saudi Arabia in 1955–56, a slight variation was introduced, as it was not necessary to expose the froth-plugs in order to locate the egg-pods (see also p. 461).

Most of the egg-fields from which *Trox* was recorded were only visited once, but a few were visited twice. At an egg-field nine miles south of Khumra, Saudi Arabia, daily observations were made from 16th January to 10th February 1956.

On several occasions, larvae collected in the field were placed in glass tubes, 4″ × 1″, and the rate of development observed. Attempts to rear adults from eggs failed, as eggs transferred to tubes containing soil did not hatch. One adult and one second-instar larva were obtained from a batch of first-instar larvae placed in tubes and a few adults have been reared from third-instar larvae.

The egg (fig. 1), the lateral view of the first-instar larva (fig. 2) and the three views of the pupa (figs. 10–12) were drawn from specimens preserved in alcohol. The spiracle (fig. 6) and antennae and mouth-parts (figs. 3–5) of the first-instar larva were drawn from permanent preparations stained with benzo-purpurin.

Distribution, Identification and Notes on the Immature Stages.

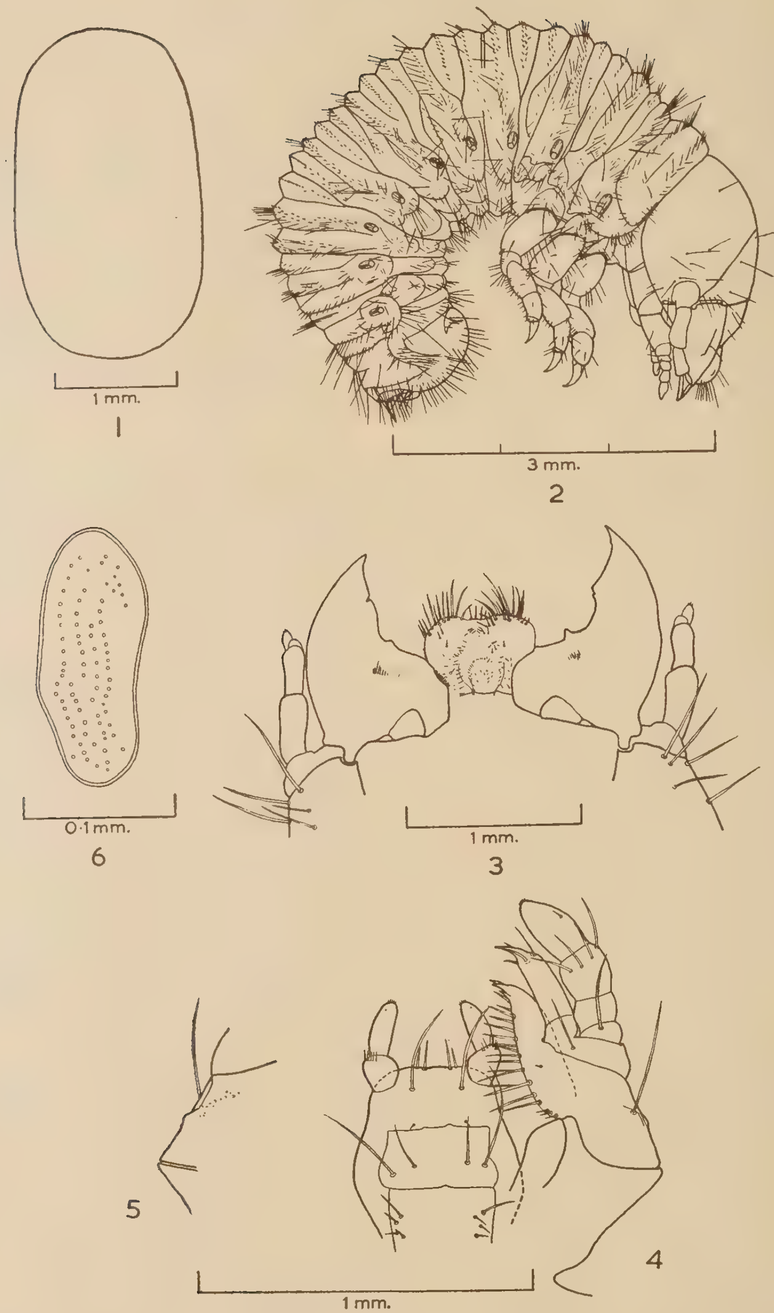
Haaf (1954) gives the distribution of *T. procerus* as Arabia, Egypt, Sudan, Ethiopia, East Africa and Senegal and in his key treats it as an African species. Gardner (1947), however, had previously recorded it from India. It is, therefore, one of the few species of *Trox* which has a range extending to two continents (Vaurie, 1955). With the exception of the observations of Gardner (1947) and van Emden (1948), these records refer to adults.

During recent investigations of the egg-fields of the Desert Locust, the early stages have been seen, in addition to adults, and in Table I the localities at which *T. procerus* has been observed in association with these egg-fields are given.

Details of the identification of the specimens of *Trox* observed in the field are also given in Table I. It can be seen that in those cases where the material has been examined authoritatively it has been determined as *T. procerus*. The certainty with which an adult of *Trox* can be identified, however, is in contrast to the difficulty of identifying the larval stage. The *radula* Erichs.–*melancholicus* Fhs. group of species, to which *T. procerus* belongs, contains 36 species according to Haaf (1954), but the larvae of only two species, including third-instar *procerus*, have been described (van Emden, 1948). Consequently, larval specimens of *Trox* cannot be identified with the same confidence as adults. For example, larvae collected in Saudi Arabia in 1955–1956 were submitted for identification to Dr. F. I. van Emden, who noted small differences between them and his description of *T. procerus* based on material collected by Hynes in Somalia in 1945, but at present it is not possible to state whether the differences noted are of specific importance.

The eggs found in Ethiopia and Eritrea have not been shown conclusively to be of *T. procerus*, but, at the Shaba egg-field, eggs containing well developed embryos were found close to recently hatched first-instar larvae, known to be *T. procerus*.

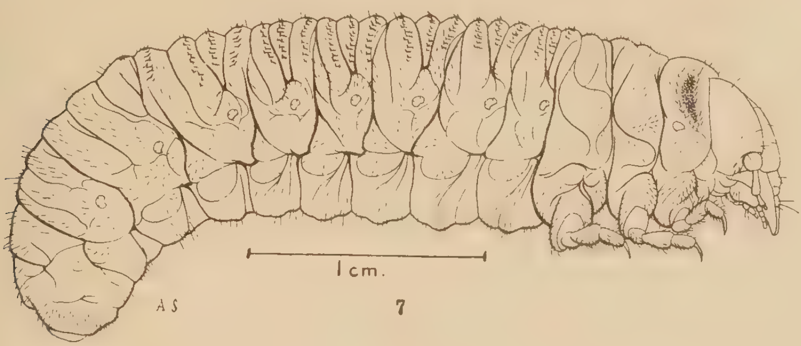
In Table I, several records of larvae seen in egg-fields of the Desert Locust have been included, although specimens were not collected and identified. Justification for the inclusion of these records is based either on the observer's statement that the larvae appeared to be in general form similar to larvae known to be of *T. procerus* and that they were behaving in a manner typical of *T. procerus*, or on the probability that any insect larva found in such an egg-field described as large and white is likely to be of *Trox* and on evidence such as behaviour and size probably of *T. procerus*, since fully grown larvae of *T. procerus* are considerably larger than any other well-known insect predator of locust eggs.

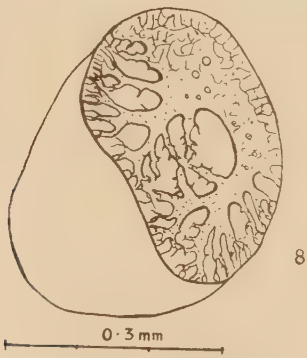


Figs. 1–6.—*Trox procerus*, egg and first instar. (1) Egg, dorsal view. (2) First instar, lateral view. (3) First instar, antenna, mandibles and labium, ventral view. (4) First instar, left maxilla and labrum, ventral view. (5) First instar, left maxilla, dorsal view showing fine skin-asperities. (6) First instar, left first abdominal spiracle showing four irregular rows of struts.

The egg (fig. 1).

The eggs available for examination were collected at Shaba and preserved. They contain well-differentiated embryos and have already become kidney-shaped in lateral view. They are about 3 mm. long and 2 mm. wide. There appears to be no sculpturing on the chorion and the micropyle has not been observed.





Figs. 7–8.—*Trox procerus*, third instar. (7) Lateral view. (8) Left spiracle of first abdominal segment.

The larva (figs. 2–8).

The third-instar larva of *T. procerus* was briefly described by Gardner (1947) who also figured the maxilla and the spiracle. Van Emden (1948) gave the diagnostic characters of *Trox* larvae (at each taxonomic level) and listed the characters by which *T. procerus* differed from *T. scaber* (L.). He also figured the spiracles of these two species and of *T. costatus* Wied.

The first-instar larvae, from which figs. 2–6 were drawn, were collected at Shaba and were recently hatched. They appear to differ from the description of the first-instar larva given by van Emden in the following respects:

Head without rugosities or shallow depression, light-sensitive areas undeveloped. First antennal segment longer than, but not twice as long as, second; third about equal in length to basal diameter of second. Dorsal surface of maxillary stipes with two irregularly arranged rows of fine skin-asperities on apical margin of sclerotised part. First thoracic segment bearing two rows of setulose hairs, posterior row more regular than anterior. Second and third thoracic segments each with two transverse dorsal folds, the anterior fold with a distinct row of setulose hairs, the posterior fold with a shorter row of spine-like setae and setulose hairs, which are more numerous on the mesothorax than on

the metathorax. On the anterior dorsal fold of the meso- and that of the metathorax there is a pair of small chitinous peg-shaped egg-bursters in a dorso-lateral position slightly anterior to the row of setulose hairs, level with the lateral ends of the rows of spine-like setae on the posterior dorsal folds. The egg-bursters are more prominent on recently hatched larvae than on larvae that have fed and grown a little. Abdominal segments with three dorsal folds; numerous setulose hairs on all middle and posterior dorsal folds and on the anterior dorsal folds of all segments posterior to the seventh. On the posterior segments setulose hairs somewhat longer. Spine-like setae on all dorsal folds of the first six abdominal segments. Ventrites with numerous setulose hairs, but no spine-like setae; on first four segments in two bands, a median anterior band of small setae and a posterior band broadly interrupted medially of longer setulose hairs. On posterior segments a single band of mainly long setulose hairs. The tenth segment with numerous setulose hairs of variable length all round, not in definite rows. Lateral callosity on each abdominal segment somewhat divided into a smaller anterior and a larger posterior area. Trochantin subdivided vertically into an anterior portion bearing one setulose hair on the prothorax but none on the meso- and metathorax, and a posterior portion bearing several setulose hairs on all three segments. Spiracular plate cribriform with four irregular rows of struts.

The second-instar larva resembles the early third instar as described by van Emden (1948). Later third-instar larvae undergo certain changes, developing some pupal features. The body, which in early third-instar larvae is uniform in

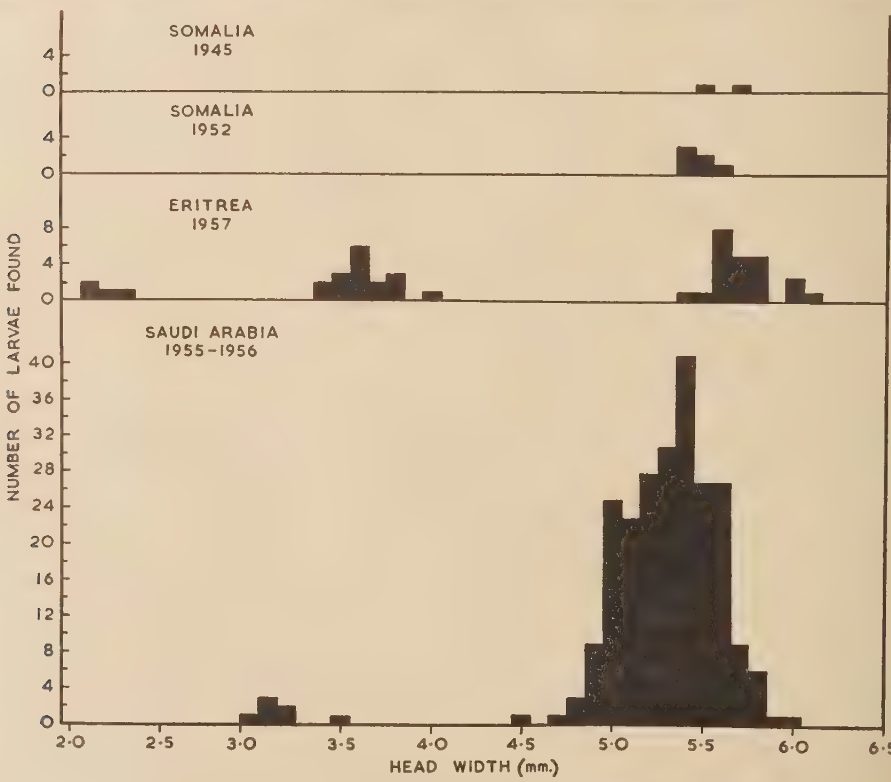


Fig. 9.—*Trox procerus*, head-widths of larvae.

width, becomes relatively wider anteriorly, the posterior end contracting, and there is an overall decrease in volume. At this time the larva may be regarded as a prepupa.

The first-instar larvae studied vary in length from about 4 mm. to 8 mm., the second-instar from 10 mm. to 20 mm. and the third-instar from 12 mm. to about 32 mm. (all measured in contracted condition).

The head-widths of the larvae collected are shown in fig. 9.

The pupa (figs. 10–12).

Denier (1936) gave a brief description and photograph of the pupa of *T. suberosus*, but the pupa of *T. procerus* has not hitherto been described or figured. The following notes are based on one specimen reared from a third-instar larva collected at Ailet.

The pupa is exarate. The integument is soft. In general form, it is much closer to the adult than to the larva. The head lies under the pronotum and therefore has a ventral aspect. There is a certain degree of asymmetry in the shape of the head and its appendages and in the arrangement and number of setae. Compound eyes clearly defined but ocelli absent. Pronotum well developed; elytra large, almost completely overlying wings. The ensheathed middle and hind tarsi bear one and two setae, respectively. Abdominal segments 1–7 dorsally, and 2–7 ventrally, unspecialised. Eighth tergite large; eighth sternite small. The gonopore, which is surrounded by sclerotised plates, is situated on the ninth sternite. Dorsal and lateral to the ninth sternite, the ninth tergite is developed into a pair of large annulated palps, fleshy basally and sclerotised apically. Between the palps lie the anus and the reduced tenth segment. There are eight spiracles, only those on the first four segments being functional. The first is covered by the elytra.

Biology.

Trox spp. have been recorded from a variety of habitats as both larvae and adults. Hayes (1930) states that the larvae are scavengers and are usually found in dried decomposing animal matter or on the soil under such matter, and Vaurie (1955) mentions some of the situations in which adults have been found, including dry carcasses, birds' nests, burrows of small mammals, and excrement.

Habitat.

The distribution of the localities from which *T. procerus* has been taken shows that the species lives in the arid and semi-arid regions of northern Africa and south-west Asia, which are characterised by high mean annual temperature and low seasonal rainfall. Such a climate imposes an essential xerophily on the vegetation; nevertheless, the vegetation varies considerably, from open woodland to sub-desert scrub and grassland. *Trox* has not been found in areas from which perennial vegetation is completely absent. Information relating to the collecting of specimens suggests that *T. procerus*, in common with other species of the genus, does not require a very limited and special micro-habitat. In Eritrea, Greathead (*in litt.*) has observed adults feeding on scraps of animal matter such as desiccated locusts, ligaments on camel bones, and dung.

The eggs and larvae have been recorded only from egg-fields of the Desert Locust, which are themselves typically confined to arid and semi-arid regions. At the time the locusts oviposit, the top soil is usually moist, but *Trox* larvae are apparently able to develop when the soil is dry (see p. 462; egg-fields in Kenya in 1955). Hynes noted that the larvae were normally in soft soils and were absent from very hard soil, in contrast to the Bombyliid, *Systocchus somali* Oldroyd, which was commonest in hard soils and almost absent from soft sandy soils (Hynes, 1947). In Saudi Arabia, the egg-fields in which *Trox* larvae were

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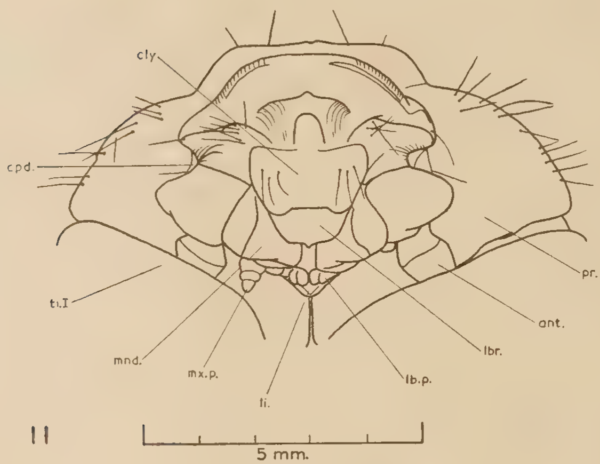

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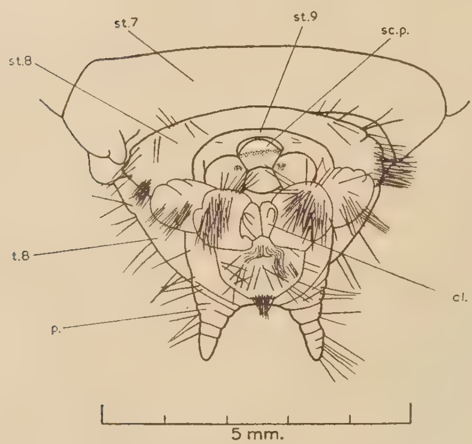

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Figs. 10–12.—*Trox procerus*, pupa. (10) Lateral view. (11) Ventral view of head and prothorax, showing arrangement of setae: ant., antenna; cly., clypeus; cpd., compound eye; lb.p., labial palp; lbr., labrum; li., ligula; mnd., mandible; mx.p., maxillary palp; pr., pronotum; ti.I, tibia of first leg. (12) Posterior end of abdomen of female, ventral view: a.l., anal lobes; p., palp; sc.p., sclerotised plates surrounding gonopore; st.7, st.8, st.9, sternites of seventh, eighth and ninth segments; t.8, tergite of eighth segment.

found were laid in areas of which the vegetation has been described by Vesey-FitzGerald (1955) as tussock-grass savannah on aeolian deposits. The top soil was characteristically soft, coarse- and medium-grained sand. At the egg-fields in Eritrea, soils ranged from hard, gravelly silt (Sheb I) to wet, loosely compacted sand (Akbanazuf). At Ado, *Trox* was confined to the soft, sandy bank at the side of a road.

Fig. 13.—*Trox procerus*. Adult, dorsal view. (× 4.)

Life-history.

As stated above, adults of *T. procerus* (fig. 13) do not appear to be restricted to a particular micro-habitat, and although they have frequently been seen in localities where there are egg-fields of the Desert Locust, and have occasionally been observed feeding on dead locusts, there is no evidence that the adults themselves are dependent upon locusts for survival. It is unfortunate that there are no observations on the behaviour of the adults of *T. procerus* before and at the time of locust oviposition. However, the observed close association between eggs and larvae of *Trox* and eggs of the Desert Locust suggests that, in areas where mature and laying swarms are present, adult *Trox* are attracted to adult locusts and it seems probable that at least some adult *Trox* lay at the time of locust oviposition. At the egg-field nine miles south of Khumra, adult *Trox* were not seen four days after oviposition by locusts, yet they had obviously been present in considerable numbers at the time of or shortly after oviposition, since successive larval instars were observed within a few days of it (Table II).

The number of eggs laid by each female and the duration of the oviposition period are not known, but at the egg-field at Shaba about five eggs and six recently hatched first-instar larvae were found within a few centimetres of one another. Although it is possible that some eggs and larvae may have been destroyed by the first larvae to hatch, it seems likely that the eggs are laid in batches that are small; this seems to be supported by the large size of the eggs. At Ado, eggs were found in tunnels made by adults, while at Ged-Ged and

Shaba they were in the soil at the bottom or to the side of locust egg-pods. The duration of the egg stage is short, probably 2–3 days, under favourable conditions. At Shaba, recently hatched first-instar larvae were found 3–4 days after locust laying. The data obtained from field observations (egg and larval stages) and rearing experiments (pupal and adult stages), relating the stage of development reached with the number of days elapsing since locust oviposition, are summarised in Table II.

TABLE II.

Stage of development reached by *Trox* in relation to the number of days elapsing since locusts oviposited in the area.

Stage	Number of days after locust oviposition when the given stage was first observed	Number of days after locust oviposition when the given stage was last observed
Egg	3	12
First-instar larva	3	12
Second-instar larva	8	21
Third-instar larva	7	25
Pupa	*ca.* 34	*ca.* 60
Adult	*ca.* 60	

Although the figures given in Table II represent extremes, taken from all egg-fields, an egg and a third-instar larva were found at a single egg-field (Ged-Ged) on the same day, which suggests that adult *Trox* do not necessarily all lay at the same time. It therefore seems likely that individual females lay repeatedly in the same egg-field or that some females lay only some days after the locusts have oviposited.

After the eggs have hatched, the first-instar larvae apparently do not move far, probably because they hatch close to a source of food. At Shaba, there was considerable variation in the size of first-instar larvae present, but no damage to locust egg-pods could be detected. Feeding in the first instar, however, undoubtedly occurs and it is possible that the earliest larvae to hatch had eaten some of the eggs or younger first-instar larvae.

The duration of the first and second larval instars is short, the third appearing as early as seven days after the locusts have oviposited; rapid growth continues in the third instar so that about 14 days after locust laying, when the locust hoppers emerge, the larvae are fully fed and have reached their maximum size. The larvae do not feed continuously but during the second instar begin to wander about in the soil, leaving tunnels behind, the position and direction of which provide information on the behaviour of larvae. Larval movement may roughly be divided into vertical and horizontal movements. Vertical movements often occur as a result of the progressive destruction of egg-pods and sometimes also of froth-plugs, but also frequently take place at the side of egg-pods. As a result of upward movement, the larvae reach the soil surface and produce characteristic mounds (see Pl. XVI, fig. 1). In their general appearance, the fresh mounds are rather similar to earthworm casts, being approximately conical in shape, with a basal diameter of about 10 cm. and a height of about 3 cm. They are formed of loose soil pushed up by the larvae, but it is not certain whether the soil is pushed up ahead of the larva as it ascends, or pushed out behind as it descends. The larvae do not appear on the surface of the soil, the material for the mound being forced up through cracks in the soil. The initial production of mounds appears to occur at a certain stage in the life-history of the larva. At the egg-field nine

miles south of Khumra, no trace of *Trox* was found between 16th and 22nd January, despite intensive sampling of egg-pods, but on 23rd January a large number of mounds suddenly appeared in another part of the egg-field and large numbers of second- and third-instar larvae were found in the soil. The mounds seem to be produced shortly after the beginning of the second instar. They are not merely the natural result of the movement of larvae ascending within egg-pods, since many mounds have been seen above larvae in tunnels having no direct connection with an egg-pod. The mounds are perhaps the result of vertical tunnelling and may act as ventilation shafts.

In Saudi Arabia, the presence of mounds was so closely correlated with the presence of second- and third-instar larvae that it was possible to state whether or not an egg-field was infested by *Trox* without resorting to digging, and, on occasion, it was even possible to locate the egg-fields themselves. The number of *Trox* larvae present in an area could be estimated by counting the number of mounds, although the number of days that had elapsed since the first mounds appeared had to be taken into account. On certain types of soil, however, mounds may not be clearly visible, since they tend to decrease in size owing to soil compaction and wind action. At the Khumra egg-field, mounds continued to be produced for about 12 days, throughout which time larvae were found close to the soil surface.

The horizontal movements appear to take place when larvae, having destroyed one egg-pod, wander in search of another. The extent of horizontal movements probably depends upon the density of egg-pods, but in Saudi Arabia no larvae were found more than 30 cm. from an egg-pod.

The locust eggs hatch 10–15 days after oviposition, with the result that the hitherto ample food supply for *Trox* larvae disappears. By this time, nearly all larvae are in the third instar and are fully fed. At Khumra, the hoppers hatched from 27th to 30th January; after 26th January, 181 third-instar and 2 second-instar *Trox* larvae were found. At the time when the hoppers hatch, the third-instar larvae undergo a definite change in behaviour. Whereas larvae are usually found in the topmost 30 cm. of soil while the locust eggs are in the ground, at the time when the hoppers hatch the larvae begin to descend in the soil, and, at the Khumra egg-field, larvae were found in tunnels running down from the top soil to a depth of over 50 cm. This descent probably marks the end of the active larval stage since larvae kept in tubes at this time made cells and became prepupae. Pupation takes place about 15–20 days after the descent of the third-instar larvae, and the adults emerge after a further period of about 25 days. Pupae and young adults have not been seen under natural conditions, and the length of life of adults is unknown.

Destruction of locust eggs.

The only stages in the life-cycle of *T. procerus* that have been observed feeding on the eggs of the Desert Locust are the second- and third-instar larvae. First-instar larvae probably also feed on them but on the few occasions when they have been seen, no damage to locust eggs could be detected. The fact that adults have not been recorded feeding on locust eggs is perhaps surprising, as the adults of three other species of *Trox*, *T. suberosus*, *T. squalidus* and *T. gemmatus* are known as egg predators, whereas, of these, only *T. suberosus* is known to feed on eggs in the larval stage as well.

The degree of destruction caused by larvae of *T. procerus*, on each occasion that it has been observed, is recorded in Table I; the total estimated egg mortality due to other causes is also given, for comparison. It can be seen that the damage caused by *Trox* varies very considerably from one egg-field to another, ranging from almost complete destruction of groups of egg-pods at Khumra and Wadi Halatha (but see p. 463, para. 6) to lack of damage at the egg-field nine miles

north of Mozheilet, Akbanazuf and Sheb II. Even in the egg-fields in Kenya in 1955, where *Trox* larvae were reported to have been present in large numbers and probably caused considerable damage, another factor, lack of soil moisture due to the failure of the rain, was of overriding importance.

The larvae attack egg-pods singly. The initial position of the first-instar larva appears to depend upon where the egg was laid and this determines the direction from which the egg-pod is attacked. Individual eggs are attacked one at a time and are completely destroyed; on no occasion were traces of yolk found. The method by which eggs are devoured without yolk escaping is unknown, since very few larvae have been found actually attacking egg-pods and feeding ceases immediately on exposure. Attacked egg-pods are often completely destroyed, and sometimes the froth-plugs are also destroyed. At the egg-fields at Khumra and Wadi Halatha, traces of egg-pods were found in which all the eggs had been eaten; frequently, however, some healthy eggs remained although these were sometimes very scattered, horizontally and vertically. At Wadi Halatha, single locust eggs and small groups of eggs were found at depths of up to 25 cm., and, at this egg-field and at Khumra, eggs were found scattered along horizontal tunnels (see Pl. XVI, fig. 2). The scattering of locust eggs appears to result from eggs becoming detached from the main mass when it is attacked by a larva; they then fall down the tunnels or are pushed along them.

After a larva has attacked one egg-pod, it presumably wanders around in the soil until it locates another. Destruction of egg-pods continues until all are destroyed or the hoppers hatch from those which escape attack (Table III).

One of the consequences of the total destruction of egg-pods and of scattering of eggs from single pods is that it becomes increasingly difficult to determine the

TABLE III.

Daily estimates of the destruction of eggs of the Desert Locust at the egg-field 9 miles south of Khumra.

Date	24.i.	25.i.	26.i.	27.i.	28.i.	29.i.	30.i.
Number of egg-pods originally present in the sample	50	38	27	20	18	7	16
Number of egg-pods damaged but not completely destroyed	27	30	24	18	11	0	4
Number of egg-pods completely destroyed	1	0	2	0	6	7	12
Number of larvae found	29	38	42	18	23	6	11
Estimated number of eggs originally present ..	3435	2611	1855	1374	1237	481	1099
Estimated number of eggs destroyed by *Trox* larvae	1214	1092	1596	741	1039	481	825
Estimated percentage destruction of eggs by *Trox* larvae	35·34	41·82	86·04	53·93	83·99	100·00	75·00
Estimated percentage mortality due to other causes	3·17	3·06	1·19	1·53	0·57	0	0·09
Average number of eggs eaten per larva per hour ..	0·27	0·16	0·19	0·18	0·18	0·29	0·25

number of egg-pods originally present and therefore the degree of destruction caused.

At the egg-field nine miles south of Khumra, daily estimates were made of the degree of destruction caused by *Trox* and other agents and the results are summarised in Table III. On 24th January, 0·69 sq. m., and from 25th to 30th January, 0·84 sq.m., were examined for each sample.

In calculating the number of eggs eaten per larva per hour it has been assumed that destruction started at midnight on 17th–18th January and the destruction on each day is calculated as for noon. The relative constancy of the number of eggs eaten per larva per hour indicates that the larvae continue to feed until the immediate food supply is greatly diminished, and that the proportion of time spent feeding remains roughly constant. The figures also suggest that eggs are eaten at the rate of only 1 every 4–5 hours, and this may account for the very small number of larvae which have been seen actually feeding on the locust eggs. Further, the figures indicate that the daily fluctuation in percentage predation reflects the number of larvae present and the food supply available, rather than real differences in feeding rates.

Of the factors other than *Trox* larvae which caused egg mortality at Khumra, the larvae of *Stomorhina lunata* (F.) were the most important. When first observed in the egg-field on 17th January the pupal stage had already been attained, but prior to this date the larvae had induced egg mortality estimated at 8·4 per cent., this figure being based on the egg-pods examined before 23rd January. It is of interest that, although pupae of *S. lunata* were locally common in groups of egg-pods examined before 23rd January, only four pupal cases were amongst egg-pods examined between 24th January and 1st February. This suggests that, if *Trox* larvae are present in an egg-field in which *Stomorhina* larvae or pupae or any other soft-bodied predator is also present, the *Trox* larvae are likely to destroy the other predators in addition to locust eggs.

Egg inviability and egg mortality caused other than by *Trox* and *Stomorhina* amounted to an estimated 0·9 per cent.

The impressive mortality figures given in Table III cannot, however, be considered representative of the whole egg-field, as the sample sites were selected because of the presence of mounds. Thus, before 23rd January, over 800 egg-pods were examined and no *Trox* larvae were found, while on 31st January and 1st February, in an area with *Trox* mounds, 171 of 485 egg-pods had been damaged by *Trox* larvae; throughout the whole egg-field, *T. procerus* probably destroyed about 30 per cent. of the eggs. The very high percentage destruction of locust eggs at the egg-field at Wadi Halatha was determined after examination of two small groups of egg-pods over which mounds were seen, and again probably did not represent the average destruction throughout the egg-field.

The data available so far seem to suggest that *T. procerus* may be an important factor in the destruction of eggs of the Desert Locust in certain seasons and in certain areas, but that generally it is not of decisive importance.

Discussion.

The contrast between the non-specialised habitats and feeding habits of the adults of *Trox procerus* and the apparently invariable and close association of its eggs and larvae with the egg-pods of the Desert Locust leads to the suggestion that *Trox* adults are attracted to areas where there are mature or laying Desert Locusts. Thus, at the egg-field nine miles south of Khumra, the density of second- and third-instar larvae, up to 42 per 0·84 sq. m., indicates that mature adults of *T. procerus* were present at some time in numbers considerably in excess of those that would be expected in the absence of locusts. The factors responsible for the concentration of *Trox* adults at Desert Locust egg-fields are not known, since their behaviour before and at the time of locust laying has not been

observed. A possible mechanism is, however, suggested by consideration of the behaviour of adult locusts at this time. Although Desert Locust swarms characteristically displace for very considerable distances (Rainey, 1951), long distance flights cease shortly before laying and swarms remain within relatively restricted areas. During this period, which lasts for only a day or two, the locusts successively pair, copulate, march or crawl in pairs, probe, etc. (Popov, *in press*). In the period before and during laying, many locusts die, and it is suggested that *Trox* adults in the vicinity of a slowly moving or settled swarm follow the locusts, feeding on the dead, so that eventually the adults of both species concentrate in groups. Thus, or in some similar way, the adults of *T. procerus* may utilise the favourable conditions of soil moisture and ample food supply with which Desert Locust egg-fields are associated. Whether there is an obligatory dependence of the larval stages of *T. procerus* upon the eggs of the Desert Locust is not known, but from general considerations of the biology of other species of *Trox* this seems unlikely.

It is emphasised, however, that *T. procerus* is the only species of *Trox* of which the developmental stages have been found in egg-fields of the Desert Locust; the evidence so far available suggests that the early stages may even be confined to such egg-fields. Moreover, the distribution of *T. procerus* is roughly comparable with that of the Desert Locust, and *T. procerus* has never been recorded outside the invasion area of this locust.

Summary.

Published records and recent unpublished field observations on *Trox procerus* Har. in Asia and Africa are assembled. All stages of the life-cycle are figured, and brief descriptive notes on the egg, larval and pupal stages, are given. It is pointed out that the egg and larval stages have only been recorded from egg-fields of the Desert Locust, *Schistocerca gregaria* (Forsk.), and that the larvae feed on the eggs of the locust, sometimes causing considerable mortality. In contrast, the adults appear to survive independently of the locust, and it is suggested that the apparent concentration of adults of *T. procerus* in areas where Desert Locusts are ovipositing is due to their being attracted to the numerous dead locusts that are present in such areas.

Acknowledgements.

I wish to record my indebtedness to Dr. P. E. Ellis, Dr. H. B. N. Hynes, Mr. C. E. S. Rennie and Miss Z. Waloff for permission to make use of their hitherto unpublished field observations; to Mr. R. A. Hall for his valuable assistance in making the observations in Saudi Arabia; and particularly to Mr. D. J. Greathead for permission to make use of his field data and for many valuable discussions.

My thanks are also due to Dr. F. I. van Emden of the Commonwealth Institute of Entomology for valuable advice on the preparation of the descriptions and figures of the first-instar larvae, to the Royal Entomological Society of London for the loan of the blocks of the third-instar larva and the adult, to Dr. B. P. Uvarov, C.M.G., F.R.S., for allowing me facilities at the Anti-Locust Research Centre during the preparation of this paper, and to Dr. T. H. C. Taylor and Mr. P. R. Stephenson, O.B.E., for the interest that they have shown throughout the work.

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DENSITY DISTRIBUTIONS OF HOPPERS OF THE RED LOCUST, *NOMADACRIS SEPTEMFASCIATA* (SERV.) (ORTH., ACRID.), IN RELATION TO CONTROL BY INSECTICIDES.

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Locusts are economically important because of their very high density in swarms of adults or bands of hoppers so that, when a crop is attacked, it is often completely destroyed. It is, however, this high density that can make the cost of killing each locust low, for the expenditure of insecticide depends mainly on the extent of the area treated. In the Red Locust, *Nomadacris septemfasciata* (Serv.), there is no indication of substantial emigration from the outbreak areas by isolated individuals, and the formation of swarms precedes emigration. It is therefore desirable to allow some congregation, so as to economise insecticide, but not to allow it to go so far that swarms emigrate before they can be destroyed. Consequently a study of the process of swarm formation is required to enable rational plans to be made.

It has already been shown that dispersed adults of the Red Locust in the outbreak areas spontaneously congregate into swarms (Scheepers & Gunn, 1958). Since the parent locusts tend to disperse again before laying eggs (Scheepers & Gunn, 1958), it is not usual to find large dense bands of hatchlings, but rather an extensive scattered infestation, naturally with variations in density. The present study concerns the hoppers, to see if they show the same tendency to concentrate, which would have the effect of producing, immediately after the last moult, adult swarms from hoppers that were originally more scattered.

It has been mentioned that the cost of insecticide treatment depends *mainly* on the area treated, but it does also increase as the sizes of the individual locusts increase, at any rate when contact insecticides are used (Gunn, 1952*a*; Gunn, Lloyd & Davey, 1954). Consequently, if the number of locusts in a band remains constant during growth, without change of area, the economical time to attack is as early as possible; if the area increases as the locusts grow, the argument would apply more strongly. If, on the other hand, initial bands grow by picking up scattered hoppers, so that a higher mortality over the whole area of infestation becomes feasible, this consideration might outweigh considerations of the relative costs of attacking only hoppers at certain stages, because big economies might be effected by avoiding the need to attack adults, which are in any case usually more spread out.

Some data are available for other species of locusts. According to Plotnikov (1931), two particular bands of the Moroccan Locust, *Dociostaurus maroccanus* (Thnb.), increased in area by about 200 times between hatching and fledging. In the Brown Locust, *Locustana pardalina* (Wlk.), which often lays eggs in dense patches or " nests ", Smit (1939) gave figures showing that the maximum density decreased to about one-tenth before emergence of the adults and presumably the target area increased by a factor approaching ten times. Such changes would have a very significant effect on expenditure on insecticides.

Although there has previously been no exact information about band formation in the Red Locust, there have been routine reports of measurements of bands attacked. The sizes vary greatly but there has been no evidence of any marked tendency for band size to increase during the two months of hopper life.

This was surprising, for it suggested that there was neither much accretion from scattered hoppers nor much spreading out horizontally as the hoppers increased in size. The data were not exact enough, however, to rely upon these conclusions; the data presented below were collected to meet that need.

General Situation.

The outbreak areas of the Red Locust and their relation to the initiation of plagues have been described by Gunn (1952*b*), Vesey-FitzGerald (1955), Backlund (1956*a*,*b*), and Gunn (1957). In 1956, control of the adult locusts had been very effective and, in order to provide material for the observations, it was decided to withhold further control in the Iku outbreak area of the Rukwa Valley, Tanganyika Territory, where there were about 12 million locusts in rather over 100 square miles (W. N. Yule & J. H. Lloyd, Observations on migration of hopper bands of the Red Locust (*Nomadacris septemfasciata* Serville) in an outbreak area (*in preparation*)). For security, from September to November an aircraft was kept working on reconnaissance and ready to attack. In November, the adults scattered and began to lay eggs (Scheepers & Gunn, 1958).

A careful survey of the area was made early in January and the most heavily infested patch, of between one and two sq. miles, was chosen. The limits of the patch were so chosen that few of the hoppers were near its edges, so allowing considerable movement before they could leave the patch. This was effective for nearly a month (fig. 1). The infestation was not the heaviest that has ever been observed but, in spite of generally poor reproduction, the observational patch was infested to a dangerous level. When the observations were begun on 18th January, the hoppers were mostly in the second, third and fourth instars; at the end, on 24th February, they were mostly in the fourth, fifth and sixth.

A rough meteorological station was set up in the centre of one of the short sides of the area. Here were recorded, every 15 min. during the observations on the locusts, the air temperature and the wind speed, taken with a hand anemometer reading in knots, the highest and lowest speeds in 100 sec. being recorded. The weather fluctuated a good deal, with skies clear or clouded, the air feeling warm or cold and damp. Nevertheless, temperatures did not alter very greatly; from 18th to 30th January the averages for 0800, 0930 and 1100 hr. were 20·7°C. (20·0–22·5°), 23·7°C. (21·5–26·5°) and 25·4°C. (23·5–27·5°) while from 15th to 22nd February the averages were 21°C. (20·0–23·0°), 24·9°C. (21·5–28·5°), and 27·8°C. (24·0–31·0°). In the same periods and times the wind averaged 100-second maxima of 1·1, 3·6, 3·7, and 0·9, 5·3, and 3·6 knots.

Methods.

A rectangular area of 1,052 acres was carefully marked out and measured by means of a Land Rover speedometer that read to 0·01 mile. It was also measured in paces and it was found that counting paces as yards gave an average error of only 1 per cent., so paces were counted as yards. The edges of the area were used by vehicles, deliberately to flatten the grass; it was hoped that this flattened grass would act as a barrier to the locust hoppers, but it was not completely effective and some interchange did take place with the surroundings. The population in a perimeter belt 100 yd. wide was roughly estimated (see fig. 1) by a daily patrol of African scouts. To mark 12 regular intervals of 200 yd. along the margins parallel to the forest edge and 6 intervals of 350 yd. along the other margins, 15-ft. poles were erected as beacons. The vegetation was almost pure, actively growing *Echinochloa pyramidalis*, with some variation in height up to 6 ft. or more. Locust infestations are often most conspicuous, if not necessarily more severe, when there is a mosaic of patches of tall species and short species of grass (Vesey-FitzGerald, 1955) but a suitable infestation in such an area was not available.

The enumerations were in two series—the radials and the zigzags. The radials were arranged at an average of 10° intervals from the centre point, actually joining the beacons to the centre. One of us (B.J.E.) generally traversed from a beacon to the centre and then to a beacon twice on each day of the recordings, thus covering four radials, and another (C.C.S.) did two radials in addition to one zigzag. The object of the radials was to estimate the relation between the scattered locusts and the bands, and in particular to see if scattered hoppers did join up into bands. Radial lines were chosen instead of parallels in order to provide data for an investigation of sampling intensity, which is not yet completed. In each of three periods, a cycle of 36 radials was completed.

The observer on the radials started by recording whether or not there were hoppers in the first 10 yd., simply + or 0, irrespective of density; this gave an estimate of the area that was clear of hoppers. For the next two yards, he estimated as closely as possible the number of hoppers in a yard-wide strip. After this, the two kinds of observation were repeated consecutively throughout the traverse. Each traverse thus consisted of continuous alternate samples of 10 yd. and 2 yd. Divided by two and averaged, the 2-yd. samples gave an estimate of the average number of locusts per sq. yd. over the whole area. From this was calculated the total number of locusts in the area.

It was impossible to count the locusts when they were very dense, and resort was had to estimation. But, in over 13,000 counts, there were only seven estimates of over 300 hoppers in two sq. yd. These few high figures very much inflate the estimates of total population for 22nd and 24th January; they were all found in the first three days and may have been overestimated. They represented very dense bands, which were followed individually up to 1st February; the bands tended to disperse and re-form but eventually lost their separate identity. We disagreed about their density, when they were very dense. There were only 14 estimates of 100–300 locusts, of which 11 fell in the first period. Apart from these, the averages per sq. yd. were based on counts and seem to have been fairly consistent and reliable.

The zigzags were done entirely by one of us (C.C.S.). The first day's course was from one corner to the middle of the opposite longer side (*i.e.*, a diagonal of half the area) and from there back again on another diagonal to the opposite corner. On each subsequent day, the course was begun at one of the beacons on the shorter side, taken at random from the beacons that had not been used as starting points, and was run parallel to the first day's diagonals in a Z-shaped course, so that on each day the equivalent of two complete diagonals were covered, usually on three straight walks. Since, at each of five beacons, the course could be begun in either of two directions, while from a corner only one direction was possible, a cycle was completed in 12 working days.

The shape of the area and the distances between the beacons were designed to give a constant length of zigzag (4,837 yd.) on parallel lines, but the daily average distance turned out to be 5,213 paces, a divergence of nearly 8 per cent. This was presumably due to the greater difficulty of walking through standing grass than around the trampled edges of the area. Moreover, over all the observations, the number of paces per day increased by 3 per cent., presumably because of the increasing height and density of the grass. Corrections for these errors might have been made, though they would have been intricate, but the errors arising from treating paces as yards are too small to affect any of the conclusions drawn from the results.

The object of the zigzags was to study changes in hopper concentrations, so isolated hoppers were ignored and a continuous population exceeding one hopper per square yard was considered as a band. This lower limit is probably too low for the hoppers to be affecting one another and far too low to be economical to control. When it became evident by looking ahead that there was a band, in

this very wide sense, the hoppers were estimated at every yard on a strip one yard wide. Neither the distances nor the numbers of hoppers were accurately found, but the accuracy was sufficient for the main purpose of estimating the numbers and sizes of such hopper bands. The widths of the bands were ignored; if a single dimension is found along a line and this is expressed as a percentage of the length of line traversed, this is a valid estimate in principle of the percentage *area* infested by bands. The problem of how to estimate the error of this percentage remains to be solved.

The radials were investigated in three separate periods (21st to 30th January, 5th to 11th February, 18th to 23rd February 1957); the zigzags were done from 18th to 31st January and 5th to 24th February. In both cases, no work was done on most Sundays.

The actual work was slow and trying. The grass was rough and often wet, soaking the observer to the skin, and canvas aprons had to be worn to prevent the grass cutting the knees. There was no shade from the sun and care had to be taken to avoid stepping into the deep cracks in the ground, for although there had been enough rain for egg-laying, there had not been enough to soak the soil and close up the dry-season cracks.

Results.

In order to test the stability of the total population of the observation area, this total was calculated for each day, using the counts made on 2 sq. yd. in every 12 yd. in the radials (fig. 1). On the graph is also shown the total population in bands, as obtained from the zigzags, the difference between the two lines representing an estimate of the numbers of locusts not in bands. Owing to the variability of the daily totals, on some days there seemed to be fewer locusts altogether than there were in bands.

On the same graph is an estimate from the records made by the African scouts of the population in bands in the 100-yd. belt around the observation area (see p. 468). This estimate is of a low order of reliability; it was made by totalling the areas of bands (sq. yd.), each measured by the scouts by two walks at right angles, and multiplying by 15, which is about the mean density of hoppers per sq. yd. found in bands in the zigzag counts within the area. From a perimeter area of about $0{\cdot}94 \times 10^6$ sq. yd. the average totals were about 16,000 hoppers and 50,000 hoppers for the first two periods of the radials, indicating that the perimeter belt was nearly empty, compared with an average of about $4\frac{1}{2}$ million locusts in $5{\cdot}09 \times 10^6$ sq. yd. within the observation area. In the third period, starting on 18th February, however, the average of the perimeter counts was 0·4 million, so that it was about half as densely populated as the main area, and on one day a maximum of 0·87 million was reached. In the first two periods, no band migration across the perimeter was observed, and drift of scattered locusts was probably as much in as out; but a big band did cross and re-cross the perimeter. This is not notably reflected in the figures of total population, presumably because of the chances of sampling. Apart from this, the observation area did seem to be reasonably self-contained.

Turning to the estimate of total population made from counts of 2 sq. yd. in every 12 yd. in the radials, the effects of the few high counts on 22nd and 24th January are very evident (fig. 1), giving totals of $25{\cdot}3 \pm 8{\cdot}4$ and $13{\cdot}5 \pm 6{\cdot}1$ millions. The pooled average for all days in the first period is $8{\cdot}35 \pm 1{\cdot}27$ millions but if the 22nd, 23rd and 24th January are omitted, the average drops to 4·56 millions, with a range of $3{\cdot}46 \pm 0{\cdot}54$ to $6{\cdot}58 \pm 1{\cdot}44$ millions. During the second and third periods, the total varied from $2{\cdot}70 \pm 0{\cdot}40$ to $6{\cdot}41 \pm 0{\cdot}67$ millions, with pooled averages of $4{\cdot}36 \pm 0{\cdot}25$ and $4{\cdot}77 \pm 0{\cdot}21$ millions for the separate periods.

The total population estimated from three periods of about a week, each containing a complete cycle of 36 radials, was thus remarkably constant; but the scatter of the daily totals is too great to be due to random errors in a randomly scattered population. With a total population of 4·56 million hoppers in the

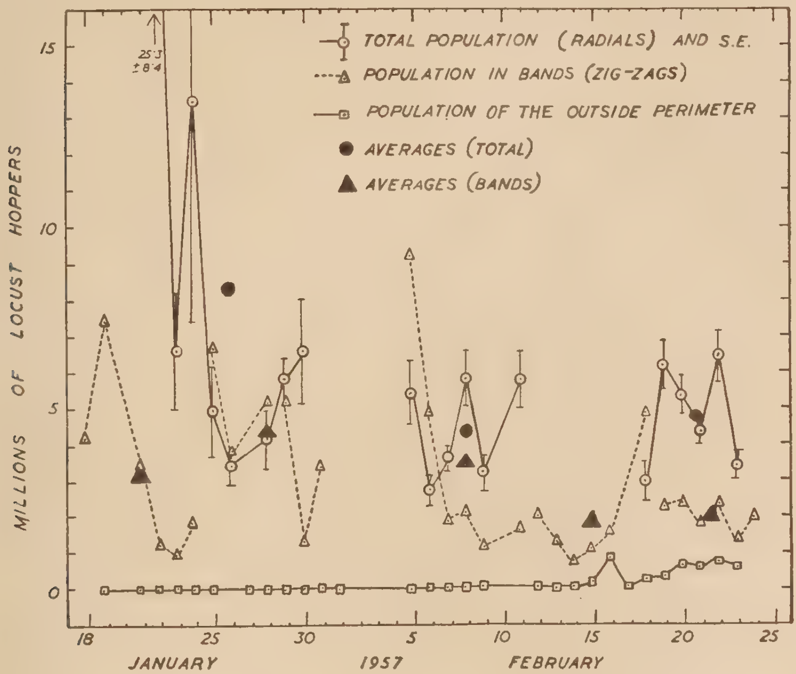

Fig. 1.—The daily total numbers of hoppers of the Red Locust in the experimental area of 1,052 acres and the daily totals of numbers in "bands" of at least 2 per sq. yd. for at least 2 yd. The bottom line shows that the perimeter belt just outside the experimental area contained very few locusts until 16th February and the main area was reasonably self-contained. Variation in the daily total was great, owing to the difficulty of sampling in the large-scale and shifting patchiness of the infestation, but the averages over complete cycles of samples (solid symbols) are reasonably consistent. There was no great change in the band structure of the population, such as has been reported for other species of locusts.

observation area, the mean density is 0·9 hopper per sq. yd. The Poisson expectation of 2-sq. yd. samples that contain no locusts is 16 per cent., compared with the actual figures of 68–75 per cent. Again, the 10-yd. values of no locusts have a Poisson expectation of 0·01 per cent. and the actual values are 61–69 per cent. Clearly there is not a random distribution of the locusts but a clumpy one. Moreover, it is apparent from the figures given that the divergence from random distribution is far greater with a 10-yd. sample than with a 2-yd. sample. Indeed, during the first period, the average number of consecutive 10-yd. samples free from locusts was nearly five (49 yd.) and the two greatest were 73 and 75 consecutive samples (730 and 750 yd.).

The analysis of figures alone gives little idea of the distribution of locusts in the observation area but to insert the figures on radial lines on a proper map would be difficult because of high frequencies of counts near the centre. Accordingly each day's figures were written down in a horizontal line and

successive lines placed below one another, so that the central points came in a vertical column. Each vertical column thus indicated densities at a certain distance from the centre. The projection was naturally much distorted but it did show that there were large locust-free areas and also higher density areas extending across several lines. Moreover, in the middle period lines 16–20 had mostly zero counts from the centre to the edge, and this wedge spread out to line 36 about half way to the edge, with few scattered locusts and only isolated high counts.

The results thus showed that there was not only a pattern of bands of hoppers on a scale that was small compared with the size of the observation area but also a pattern almost as large as the area itself, so that substantial continuous parts of the area were quite uninfested. Because of this large pattern, a single line or even several lines would not adequately sample the area, for on one day the lines might by chance go through parts of the area predominantly well-populated with locusts and on another day they might go through predominantly empty areas. The patchiness that determined the standard error was on a scale of square-yard areas, while the patchiness which so greatly affected the total was on a scale of hundreds of acres. Within each of the three periods, on the other hand, all 36 radials were used, so the large-scale patchiness was more fairly sampled and the averages for the second and third periods differ insignificantly. Lumping them together gives 4·56 ± 0·17 million, which happens to be the same as the selected average for 25th–30th January, *i.e.*, all but the first three days of the first period (see p. 470). For the future, there is evidently a difficult problem to be tackled, namely to find the most economical way of sampling an area in which the locusts are in bands and even the bands are not randomly distributed, and of determining the reliability of the sample.

In this case, however, the total number of locusts found seems to have been very constant except for the first three days. Whatever may be the explanation of the high densities recorded on those days, from 25th January the population within the observational area seems to have been constant enough for our purpose.

The daily estimate of the total number of hoppers in bands, as found in the zigzags, also fluctuates considerably. Taking five periods, each containing six zigzags, the pooled averages are 3·2, 4·3, 3·5, 1·9 and 2·0 millions, with a general average of 3·0 millions (Table III). Grouping together the first pair and the second pair, a reasonable procedure because 12 zigzags made up a cycle, gives 3·7 and 2·7 millions and it certainly looks as if the number of hoppers in bands was falling towards the end, in spite of the constancy in the total population at 4½ million. Unfortunately an estimate of reliability of these totals, suitable to

TABLE I.

Frequencies per 1,000 counts of densities of locust hoppers in 2 sq. yd. as found in the radially arranged samples in an area of 1,052 acres.

Locusts per 2 sq. yd.	22–30 Jan.		5–11 Feb.		18–23 Feb.	
	Counts	Locusts	Counts	Locusts	Counts	Locusts
0	748	0	740	0	682	0
1–9	202	614	216	693	272	903
10–29	36	573	34	532	36	552
30–99	9	472	9	439	9	409
100–299	2·4	377	0·5	69	0·2	27
300–	1·6	1272	—	—	—	—
Totals ..	999·0	3308	999·5	1733	999·2	1891

the method of collection of the data, is not easy to find. The two independent sets of results—from radials and zigzags—do, however, give consistent results (see below). Over the later observations, the proportion of the locusts in bands seems to have dropped from as high as 75 per cent. (5th–11th February) to below 50 per cent. (19th–24th February).

When the details of the radial estimates are examined (Table I) it is evident that there was no dramatic change over the three periods, such as has been recorded for other species of locusts. Once more, the very high estimates of density made in the first three days show up strikingly. Apart from that, there was an astonishing stability in the proportion of the total area occupied at each density and in the proportion of the locusts to be found at each density. There was a small reduction in the zero counts, namely 75, 74 and 68 per cent. in the three periods, and an almost exactly corresponding rise in the extent of the low densities (1–9 per sq. yd.). There was possibly a shift of locusts from the higher to the lowest densities, but its extent was not of very great importance; the rise in number of locusts at the lowest densities, which was accompanied by a rise in the total, may have been partly due, too, to better spotting, which would also explain the reduction in zeros.

The 10-yd. records of the radials gave, for the three periods, 68, 69 and 61 per cent. of zeros. It is to be expected that 10-yd. stretches without hoppers would be somewhat less frequent than 2-yd. stretches, so these figures confirm the stability of the area containing no locusts, with a slight but unimportant drop in the third period.

In these data, each 10-yd. or 2-yd. count has so far been treated as a unit, without reference to the neighbouring counts. The zigzag samples were designed to show up continuous stretches of hoppers, forming concentrations or bands. The density data are shown in Table II, classified in such a way as to facilitate comparisons with Table I.

TABLE II.

Changes in distribution of those hoppers that were in bands, as determined by the zigzag samples.

Locusts per 2 sq. yd.	18–30 Jan.		5–11 Feb.		12–24 Feb.		Means	
	Units	Locusts	Units	Locusts	Units	Locusts	Units	Locusts
2–8	9	57	23	142	6	42	10	68
10–28	13	217	28	488	15	337	17	320
30–98	13	743*	3	167	10	408	10	495
100–298	2·9	379	0·6	77	—	—	1·3	164
300–	0·2	89	1·4	522*	—	—	0·4	139
Totals	38	1485	56	1396	31	787	39	1187

* Figures higher than in Table I.

For easy comparison with Table I, the densities are given per 2 sq. yd. and the distances through bands in units of 2 yd. per 2,000 yd. walked. In the first and the last periods about 62,000 yd. of sampling were done on 12 days, while in the middle period it was half as much.

Over the whole period of the observations, there were only two cases of particular densities occurring considerably more in bands than in the general population. From 18th to 30th January, there were more hoppers at 30–98 per 2 sq. yd. in the zigzags than from 22nd to 30th January in the radials, but of course there were many more in a few yards at higher densities in the radials. Again, from 5th to 11th February the highest densities occurred in a few yards in the zigzags only, but this, too, may be due to the difficulty of fair sampling

for very small patches at very high density. Apart from these two cases, the zigzags always showed fewer locusts at a particular density than the radials, a result which indicates that very small patches occurred at most densities, patches too small to be reckoned as bands.

The two lots of data, obtained independently, are thus reasonably consistent in regard to distribution of densities. They are also consistent in indicating a progressive reduction in frequency of the highest densities (over 100 per 2 sq. yd.), although this is subject to the sampling difficulty for infrequent events. An analysis of band structure is shown (Table III) in which for convenience the total population is taken as constant, though it may well have been higher up to the end of January, so the percentages of the hoppers congregated into bands in January may be shown too high.

TABLE III.

Changes in band structure, as determined in the zigzag samples.

Date	January		February			Means
	18–24	25–31	5–11	12–18	19–24	
Per 2000 yd.						
Number of hoppers ..	1262	1693	1396	768	805	1183
Number of bands ..	8·7	4·3	3·8	3·0	1·2	4·2
Yd. thro' bands ..	71	81	113	80	43	78
Av. size (yd.) ..	8	19	30	26	36	19
Density, hoppers sq. yd.	18	21	12	10	19	15
Percentage infestation	3·6	4·0	5·7	4·0	2·1	3·9
Total hoppers in bands $\times 10^6$	3·2	4·3	3·5	1·9	2·0	3·0
Hoppers in bands as % of $4{\cdot}56 \times 10^6$*	70	94	75	42	44	65

* Estimated total population in area (see p. 472).

The numbers are given per 2,000 yd. for easy comparison with Table I.

There was a definite fall in the number of bands over the whole period. This could be attributed partly to an equally definite reduction of the number of hoppers in bands; but an increase in the sizes of bands, presumably due to fusion of previously separate bands, was equally important. During the first half of February, the bands became less dense; this was accompanied by an increase in total extent of bands during 5th to 11th February and seems to have led to some complete dispersal of bands, for from 12th to 18th February the density remained about the same but the total area of bands dropped sharply. In the final period, about the same reduced number of locusts was found at double the density and in half the area, so the surviving bands seem to have tightened up.

In the radial samples, presence or absence of hoppers was noted for each 10 yd. Referring to a 10-yd. sample as a block, for the three periods the average numbers of successive blocks with all zeros were 4·9, 7·2 and 7·0; and for locusts present they were 2·4, 3·4 and 4·5. Here again we get evidence of a coarsening of the pattern; the increases in number of successive blocks containing hoppers correspond to an increase in band size but there were evidently also increases in the sizes of patches with no locusts present.

The variation in percentage infestation is rather large (Table III). Up to the present, this has been the only measure of infestation that could be made sufficiently rapidly to be of value for control planning. The procedure has been for

a man on foot or in a Land Rover to make straight traverses and to find the percentage of the total traverse that passed through bands. A variation from 2 per cent. to 6 per cent. in a constant infestation (Table III) would seem to make the method of little value. The serious weakness of the method is that it takes no account of density of hoppers in bands, because densities take a long time to estimate. The criterion of the density that is sufficient to count as a band is important, not only in the level of the values found but also in their consistency. For example, the high value of 5·7 per cent. given for 5th–11th February is largely due to the abnormally high extent of bands at 1–4 hoppers per sq. yd., so diffuse that "band" is probably a misnomer. If only infestations in the zigzags at 5 hoppers or more per sq. yd. and at least 2 yd. across are counted, the five percentages become 2·1, 3·8, 3·4, 2·7 and 2·2, a variation of 2 to 4 instead of 2 to 6. The differences thus shown are real, for the evidence is clear that bands dispersed towards the end, while the low initial figure is due to the high proportion of the locusts that were in small thin bands. All one can say about the value of determining the percentage infestation by bands at least 2 yd. across and having 5 or more hoppers per sq. yd. is that it is better than nothing, but not very good, for a constant infestation may give a figure varying by ± 30 per cent.

Discussion.

The object of these observations was to discover whether the aggregation behaviour of hoppers of the Red Locust indicated whether insecticide attacks should be made early, when area dosages would be low, or late, when there might be more concentrated targets and fewer dispersed locusts. The results are clear enough. Although the pattern of bands and uninfested areas became coarser, counting any continuous infestation over 1 per sq. yd. as a band, the number of dispersed locusts increased. At the end, the bands were therefore larger but they did not contain so many of the locusts.

Between late January and mid-February, there was a reduction in the number of bands and their size increased more than enough to be explained by fusion of small bands into larger ones. The balance of the increase in size can be explained by the lowering of the mean density, so that the bands fused, enlarged and loosened, and it also appeared that some locusts dispersed. Between mid-February and late February, fusion, enlargement and loss by dispersal continued, but within the bands the density rose again, so the loosening process was reversed. Over the three periods taken together, there was thus a decrease in number of bands and an increase in their size, due to fusion, but there was a loss of hoppers from bands into a dispersed condition; the density within the bands first dropped and then rose again in the proportions 2:1:2.

The conclusion reached is therefore that no purpose would have been served by withholding control, for the target bands did not become much larger while the number of hoppers that were not in bands increased substantially. In any case, continuous observation showed that particular bands tended to disperse while others formed within the same high-density area, so that a somewhat prolonged attacking period would have been necessary. In fact, of course, the average size of bands was excessively small for control by normal techniques of aircraft spraying, for the highest average distance through bands was only 36 yd. This represents the length of random traverses through bands and since a traverse will often go through a narrow place in the band and can never over-estimate the distance through, the average under-estimates the greatest dimensions of bands. If the bands were of regular shape, such as circular, their average dimensions could be estimated (average traverse equals average diameter multiplied by $\frac{1}{4}\pi$), but they are very irregular in shape. The true average might be

about 50 yd. and the average area of a band therefore about 0·5 acre. The preferred target for aircraft spraying is of the order of 60 acres.

It is evident that elimination of bands alone, even including such small and loose bands as were included in these observations, could only reduce the population by about half and would require supplementing by attacks on the later adults. This corresponds to experience (J. H. Lloyd, Operational researches on preventive control of the Red Locust (*Nomadacris septemfasciata* Serville) by insecticides (*in preparation*)). Such control would delay the formation of adult swarms by eliminating ready-formed dense groups, but attacks on bands alone would be too detailed for aircraft. It looks as if the residual spraying in a lattice pattern, now being investigated by Messrs. Lloyd and Yule, is more likely to be the required control method for hoppers because of its high speed and the prospect it offers of destroying also some of the isolated locusts. A preliminary trial of this method at Iku in 1957 reduced the whole population in over a hundred square miles by the record proportion of 70 per cent.

There was evidence of a certain amount of dispersal during the observations and it might therefore be held that the locusts were not exhibiting their gregarious behaviour to the full because there were too few of them in the area (Ellis, 1951, 1953*b*). That may indeed be true but the degree of infestation (2–4%) was sufficient to require control, for the highest infestation so far recorded over such an area has been 14 per cent., while a very serious situation arose in the North Rukwa outbreak areas in 1954 when there was a 6 per cent. infestation over about 35 sq. miles. Even within the small observation area in 1957, the total number of locusts was probably just enough to form a migratory swarm. The same density of infestation over a large area would certainly have given rise to migratory swarms.

That is to say, the observations are relevant to a situation that does occur and does require control; it is not to say that a much heavier infestation would behave in the same way and the results should not be taken as having universal application to hoppers of the Red Locust. Moreover, behaviour might be quantitatively somewhat different in a mosaic area (Chapman, *in press*). In the same way, the weather is never typical of any large number of years but varies from year to year and from area to area. Further observations will therefore be necessary in the future. They may well be made by methods developed from those described here.

Although there may well be specific differences (Ellis, 1956), the key to the differences in this respect between the Red Locust on the one hand and the Moroccan and Brown Locusts on the other hand probably lies in the terrain, and the differences are well illustrated by reference to yet another species, the Desert Locust (Kennedy, 1939; Ellis & Ashall, 1957). In this species, *Schistocerca gregaria* (Forsk.), the eggs tend to be laid simultaneously and in dense groups (up to 101 pods per sq. yd.) so that the hoppers may be in very dense bands as soon as they hatch. Then there is usually a good deal of bare ground, so that hatchling bands move readily and tend to fuse. The distances travelled by hopper bands of the Desert Locust are far greater than by those of the Red Locust (*cf.* Yule & Lloyd, *op cit.*, and Ellis & Ashall, 1957), so that more opportunities for fusion occur. When, however, a band of the Desert Locust entered a dense stand of vegetation, it tended to spread out and become static (Kennedy, 1939; Ellis & Ashall, 1957).

The Red Locust differs radically from the three other species mentioned in that it inhabits plains which are densely clothed with grass and practically devoid of bare ground. Even when there is bare ground, hoppers of the Red Locust seldom rest on it, or use it, and they often seem reluctant to cross it; on only two occasions in five years have streams of hoppers in the outbreak areas been seen marching along a footpath. Band movement is due to the individual hoppers

jumping from stem to stem of the grass. Under these conditions, visual stimulation of one hopper by another (Kennedy, 1939; Ellis, 1953*a*) must be much interfered with and once a hopper by chance gets out of a band, it often could not readily see which way to return. It would be interesting to know if the African Migratory Locust, *Locusta migratoria migratorioides* (R. & F.), in its outbreak areas of the grassy flood-plains of the Middle Niger behaves like the Red Locust.

Summary.

In continuation of a study of the process of swarm formation in the Red Locust, *Nomadacris septemfasciata* (Serv.), to enable rational plans for control measures to be made, the population distribution of about 4½ million hoppers of the Red Locust was investigated in an observation area of 1,052 acres in the Iku outbreak area of the Rukwa Valley, Tanganyika Territory, from 18th January to 24th February 1957, to see if the hoppers showed a tendency to concentrate, which would have the effect of producing, immediately after the last moult, adult swarms from hoppers that were originally more scattered. From 25th January onwards, the estimated population remained constant in numbers. Densities over 50 per sq. yd. were unusual and, taking any continuous infestation over one per sq. yd. as a band, the mean density of hoppers in bands was 15 per sq. yd. There was a tendency for such bands to become larger by fusion and for the area quite free from locusts to increase slightly but the number of dispersed locusts increased. There would therefore have been no advantage in withholding insecticide control in the hope of attacking denser and more economical targets. Nevertheless, such populations have to be controlled.

In the Red Locust, under the conditions described, it seems probable that the behaviour of the young adults is most important in the formation of dense swarms, while in certain other species but not in the Red Locust, concentrated egg-laying and the behaviour of the hoppers are also important.

Investigations are required on more economical enumeration of patchy gregarious distributions.

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THE REPRODUCTION OF THE RED LOCUST, *NOMADACRIS SEPTEMFASCIATA* (SERV.) (ORTHOPTERA, ACRIDIDAE), IN AN OUTBREAK AREA.

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In any study of population dynamics, the capacity for increase of the animal concerned is of fundamental importance. In locust work this is particularly true, for, under favourable conditions, populations of these insects are capable of spectacular increases in a short space of time; this and the swarming habits make the locusts animals of serious economic importance. The present work was carried out in the Rukwa Valley, Tanganyika Territory, one of the three recognised outbreak areas of the Red Locust, *Nomadacris septemfasciata* (Serv.).

In the field, the Red Locust has only one generation per year, although in open-air cages up to three generations per year may be obtained (Albrecht, 1953). The eggs are laid at the beginning of the rainy season, usually November or December. The adults die after egg-laying, the sharp drop in population coming late in December or in January. The present work was carried out during the months of November to January 1952–53, 1953–54, 1954–55 and 1955–56.

Methods.

Each year, before the rains began, a suitable area of unburnt grass was chosen containing a fairly high but countable locust population. Every two or three days the population in the area was estimated and a sample of locusts collected. A rain gauge was set up in the experimental area and readings taken daily or whenever the area was visited. African scouts made the estimates of the population and collected the samples, the latter being taken immediately after the estimates of population had been completed. Working in pairs, one walking behind the other, the first man counted paces and the second man counted the locusts flushed by disturbance, the population being expressed in numbers of locusts per 100 paces. Although this method gives a relative and not an absolute estimate of the population, it was adequate for the present purpose.

Throughout the series of observations, an attempt was made to ensure that there were at least 100 females in each sample. In practice, this was usually found to be impossible in the time available, as at that season of the year the temperature was high and on some days the locusts were very difficult to catch. In each year also, in early January, the drop in population following egg-laying was very evident, and then the experiment had to be abandoned because only very few locusts could be caught, even though egg-laying had not ceased.

The female locusts were dissected, and the ovaries removed and classified according to the length of eggs, as follows:—

Class I	Eggs under 2 mm.
Class II	Eggs under 3 mm. but over 2 mm.
Class III	Eggs under 4 mm. but over 3 mm.
Class IV	Eggs under 5 mm. but over 4 mm.
Class V	Eggs over 5 mm.

TABLE I.

Percentages of locusts with ovaries at various stages of development in 1952 on the dates shown.

Date Sample	18/xi 46	21/xi 100	25/xi 97	28/xi 50	2/xii 74
Class					
I	61	13	—	—	—
II	15	15	8	—	—
III	11	25	12	2	—
IV	9	20	6	2	4
V	4	20	19	40	9
Ic	—	7	37	18	8
IIc	—	—	11	10	17
IIIc	—	—	6	14	22
IVc	—	—	—	6	26
Vc	—	—	—	8	15

Classes marked c had *corpora lutea*.

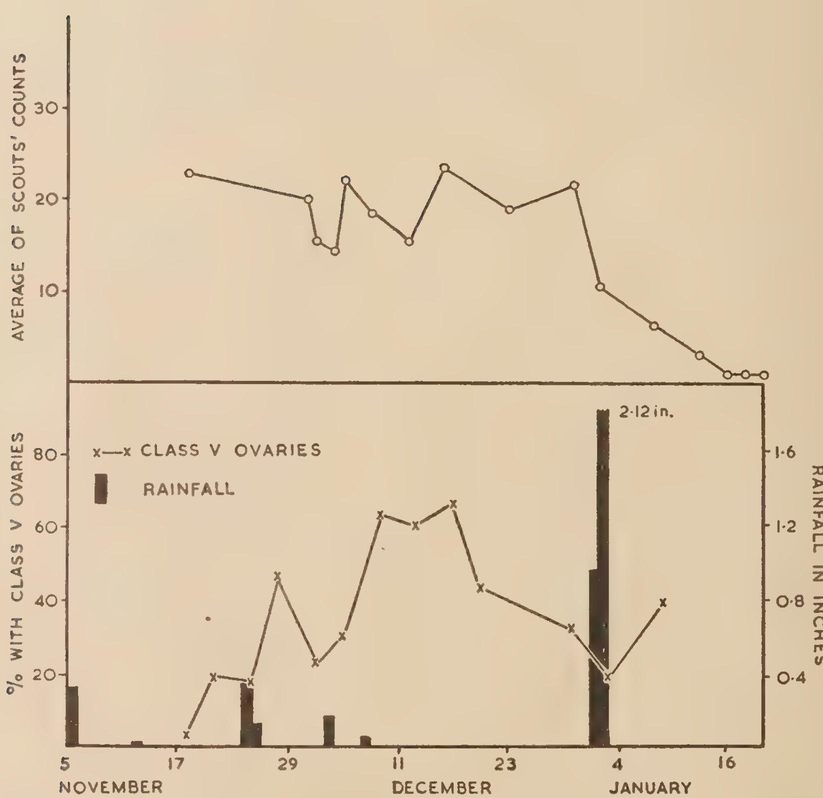


Fig. 1.—The average population level (locusts flushed per 100 paces), percentage of locusts having Class V ovaries, and rainfall, during the 1952–53 breeding season.

The eggs were measured to the nearest 0·5 mm. It was hoped that it would be possible, by inspection, to separate the ovaries into successive layings. In some cases, undeveloped and freshly spent ovaries could be distinguished by the absence or presence of the *corpus luteum* (Phipps, 1949). It was found, however, that an ovary which had released ripe eggs did not retain visible *corpora lutea* after the succeeding eggs had reached a length of 4 mm., and often the *corpora lutea* disappeared before that stage was reached. Also, it was observed that *corpora lutea* could be present in degenerating ovarioles of ovaries which were unspent. Consequently it could not easily be decided when all females had laid at least one egg-pod. Therefore, although tentative use is made below of the information on the first layings, the ovaries in a single sample are classified on the single criterion of length of eggs.

Of the five classes of egg, most emphasis has been placed on Class V, in which the eggs are regarded as being fully developed and ready for laying. In fact, Class V also incorporates a " Class VI " in which the eggs have left the ovary and are lying in the oviduct. In this final stage the length of egg is approximately 6 mm. This stage, however, seemed to be very short and comprised a very small percentage of each sample; Class V was therefore considered adequate for the purposes of the observations.

Rate of Ovary Development and its Relationship to Body Weight.

Figs. 1–4 and Tables I–IV relate to four breeding seasons. Table I shows that in 1952 the first egg-layings leading to the appearance of Class Ic ovaries (newly spent, containing *corpora lutea*) had occurred by 21st November; the percentage of locusts with Class V ovaries reached a first peak a few days later, on 28th November (fig. 1), and then dropped sharply, indicating a general laying between the 21st November and 1st December. The question whether all the locusts oviposited about that time now arises. The sharp fall in the numbers with Class I ovaries between 18th and 21st November, and the absence of any in that Class in the following samples (Table I), show clearly that none of the ovaries had remained in the dormant condition and that their development from that stage had been rapid.

It is difficult to determine how rapid the development was, but some indication may be obtained from the Tables, from which it may be concluded that eggs become ready to be laid about seven days after the start of development. Thus in the period 18th to 21st November 1952, 48 per cent. of the locusts had passed out of the Class I stage, but on 21st November there were only 40 per cent. with

TABLE II.

Percentages of locusts with ovaries at various stages of development in 1953 on the dates shown.

Date Sample	26/xi	29/xi 104	3/xii 64	6/xii 190	9/xii 160	12/xii 37	15/xii 57	19/xii 46	22/xii 9	28/xii 6
Class										
I	100	92	30	17	8	13	9	2	—	—
II	—	7	31	17	15	22	19	13	—	—
III	—	1	31	28	37	13	26	35	22	—
IV	—	—	6	20	21	24	26	26	44	16
V	—	—	2	17	19	27	19	24	11	33
Ic	—	—	—	—	—	—	—	—	22	0
IIc	—	—	—	—	—	—	—	—	—	50

Classes marked c had *corpora lutea*.

TABLE III.

Percentages of locusts with ovaries at various stages of development in 1954 on the dates shown.

Date Sample	7/xi	9/xi 119	11/xi 152	13/xi 93	15/xi 100	17/xi 92	19/xi 106	21/xi 88
Class								
I	100	93	76	19	13	4	2	—
II	—	6	19	20	25	2	2	1
III	—	0	3	16	25	18	2	5
IV	—	1	2	21	19	25	16	9
V	—	—	—	23	14	39	58	27
Ic	—	—	—	—	3	7	16	41
IIc	—	—	—	—	—	4	3	12
IIIc	—	—	—	—	—	—	1	3
IVc	—	—	—	—	—	—	—	1

Classes marked c had *corpora lutea.*

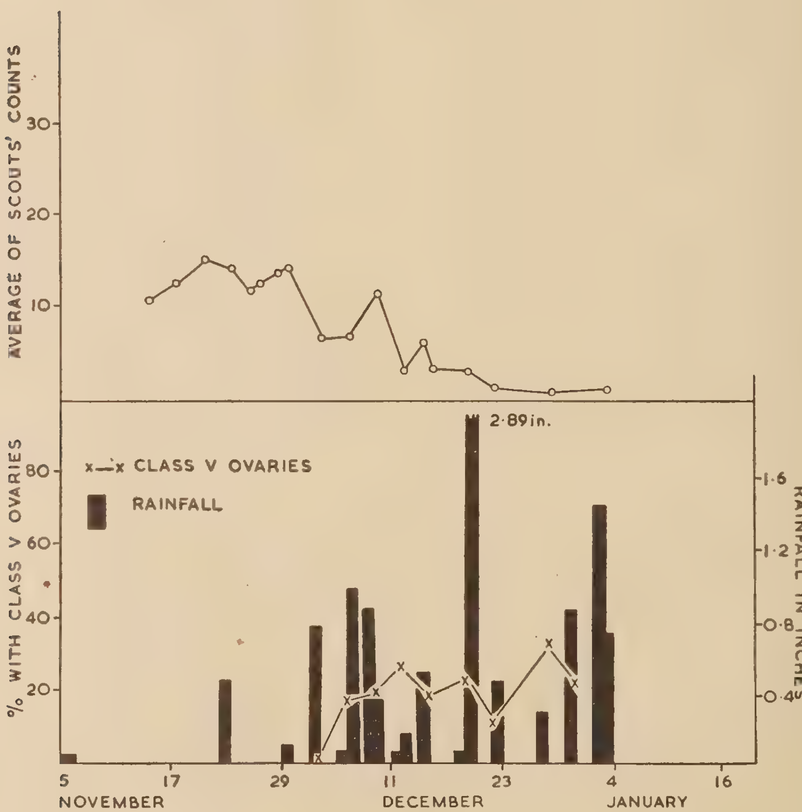


Fig. 2.—The average population level (locusts flushed per 100 paces), percentage of locusts having Class V ovaries, and rainfall, during the 1953–54 breeding season.

ovaries in Classes II and III combined (Table I). If the samples were adequate, this means that some ovaries had developed from Class I to Class IV in three days. In addition, between 21st and 25th November, the 13 per cent. in Class I on 21st November had passed into Classes II and III. Similarly, in 1953 (Table II), between 26th and 29th November, and 29th November and 3rd December, Class I ovaries had passed into Classes II and III, in 3 and 4 days, respectively; and in 1954 (Table III) from 7th to 9th November and 11th to 13th November, Class I ovaries had moved into Classes II, III and IV in two days. The duration of Classes II and III must therefore be only about a day each. This can be confirmed by an inspection of the movements of Class II and III ovaries in the Tables. The duration of Class IV can also be determined in similar fashion, and may be taken as lasting not more than 2 or 3 days.

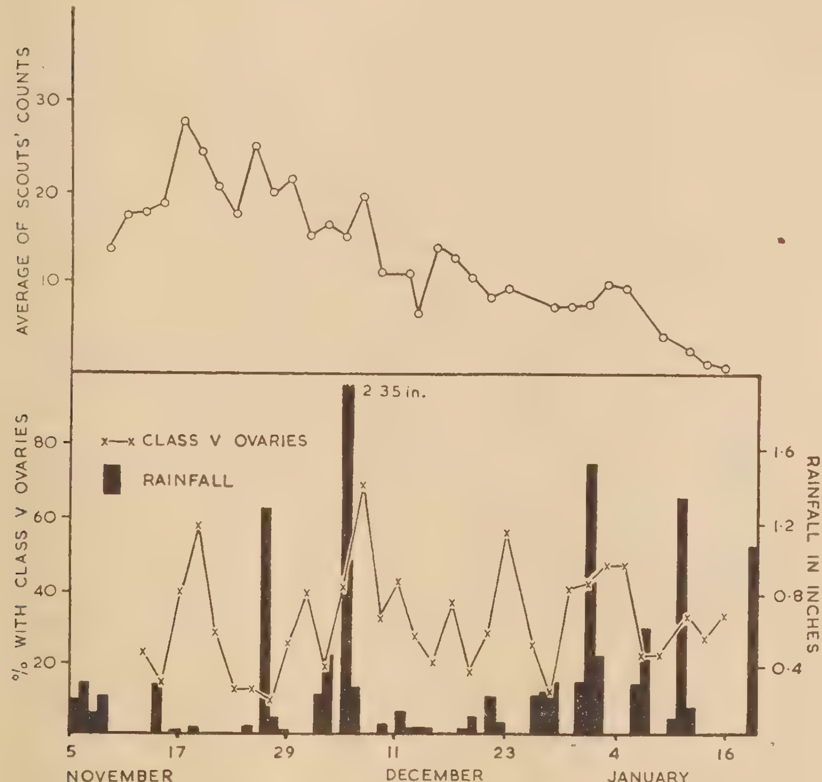


Fig. 3.—The average population level (locusts flushed per 100 paces), percentage of locusts having Class V ovaries, and rainfall, during the 1954–55 breeding season.

In the consideration of the duration of Class V ovaries, Tables I and III (for 1952 and 1954) show that Class V is of short duration, the Class V ovaries moving to Classes Ic and IIc in as short a period as two days, which justifies regarding Class V ovaries as having, for the purposes of the observations, eggs ready to lay. However, in 1953 and 1955 (Tables II & IV) an entirely different result is seen. In 1953, the first Class V ovaries appeared on 3rd December, but the first Class Ic

TABLE IV.

Percentages of locusts with ovaries at various stages of development in 1955 on the dates shown.

Date	22/xi	23/xi	24/xi	25/xi	26/xi	28/xi	29/xi	30/xi	1/xii	2/xii	3/xii	5/xii	6/xii	7/xii	8/xii
Sample		102	111	109	121	98	80	82	80	100	99	94	136	67	103
Class I ..	100	95	96	95	93	92	91	96	91	83	76	4	6	3	—
II ..	—	4	3	3	2	4	4	4	5	9	11	21	5	1	4
III ..	—	1	—	2	4	1	3	—	4	6	5	49	17	8	7
IV ..	—	—	1	—	1	2	—	—	—	2	4	16	35	22	8
V ..	—	—	—	—	—	1	2	—	—	—	4	10	37	66	68
Ic ..	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13

Class Ic had *corpora lutea*.

ovary was not seen until 22nd December. During this period, apparently negative rates of transfer from class to class were found from 12th to 19th December. Similarly in 1955, the first Class V ovaries appeared on 28th November but the first Class Ic ovary did not appear until 8th December; again, apparently negative rates of transfer were found between 26th and 30th November. The reasons for these delays in oviposition are not known, but the possible factors will be discussed below.

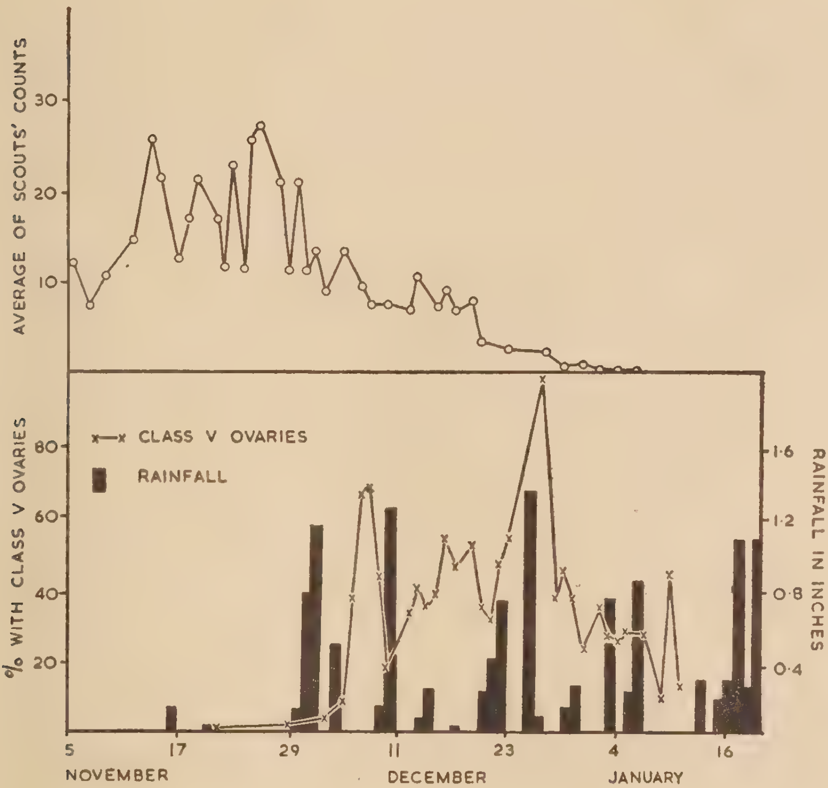


Fig. 4.—The average population level (locusts flushed per 100 paces), percentage of locusts having Class V ovaries, and rainfall, during the 1955–56 breeding season.

To obtain further evidence of the rate at which the ovaries develop from Class to Class (Tables I to IV), a number of females were weighed alive in the 1955–56 season, and the length of elytron was measured to give an indication of the size at emergence. As far as possible the locusts were caught in the early morning in an attempt to eliminate differences of weight caused by amount of feeding. The ovaries were then dissected out and classified. The object was to compile a graph showing the correlation between weight and length of elytron for each class of ovaries, and then to use this graph as a standard for relating the change in weight of individual locusts, weighed daily throughout the breeding season.

The results obtained in compiling the standard showed the expected increase of weight with development of the ovary and also showed a good correlation between weight and elytron length* (fig. 5). However, the actual regression lines obtained were close together, and the spread of points was relatively so great that it was considered to be impossible to identify the various stages of ovarian development in an individual locust from elytron length and weight alone, *i.e.*,

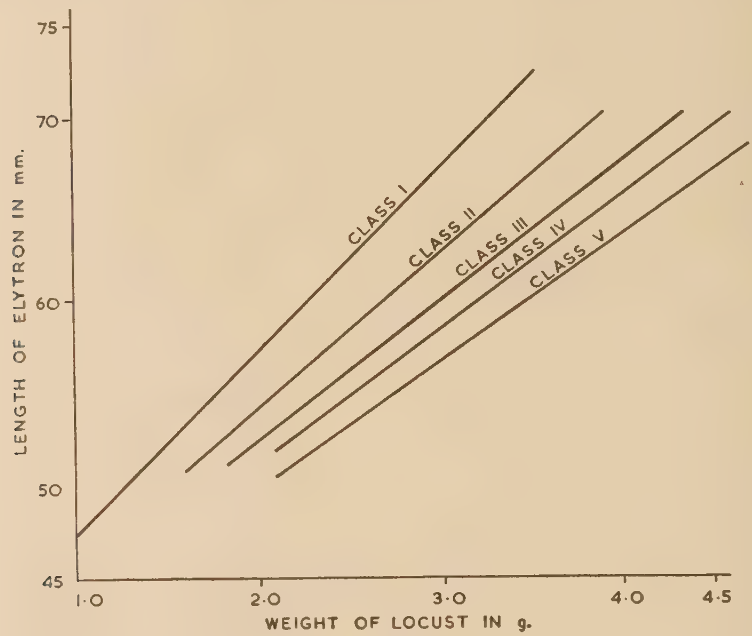


Fig. 5.—The relation between weight, elytron length and ovary development.

without dissection, especially if the specimen was kept in a cage under artificial conditions. It would be possible to separate Class I from Class V with reasonable certainty, but not the intermediates. The numbers of individuals from which the regression lines were calculated are shown in Table V.

TABLE V.

The correlation coefficients and regression lines for length of elytron and weight of locust for the five classes of ovary.

Class of ovary	No. of specimens	Correlation coefficient	Formula of regression line
I	463	0·78	x=0·102y—6·02
II	48	0·84	x=0·115y—4·154
III	62	0·84	x=0·139y—5·319
IV	81	0·89	x=0·135y—4·914
V	129	0·84	x=0·148y—5·391

x = weight. y = elytron length.

From fig. 5, a general indication of increase in weight with development of ovary can be estimated for any particular length of elytron; if the weight of a Class I ovary is taken as unity, then the percentage increase in weight of the locust for each class can be calculated. In the examples given in Table VI, namely an intermediate figure and the two extremes, it will be seen that in all cases the percentage increase is approximately the same, and it would appear that, on the average, the weight of a locust with a fully developed ovary is about one-half greater than it was before egg development began.

Factors affecting the Initiation of Ovary Development.

In figs. 6 to 8 are shown the daily maximum temperatures and relative humidities in the experimental areas around the times at which egg development started in 1953, 1954 and 1955, as well as the incidence of rain and the dates when Class II ovaries first appeared in the samples. When the data from these

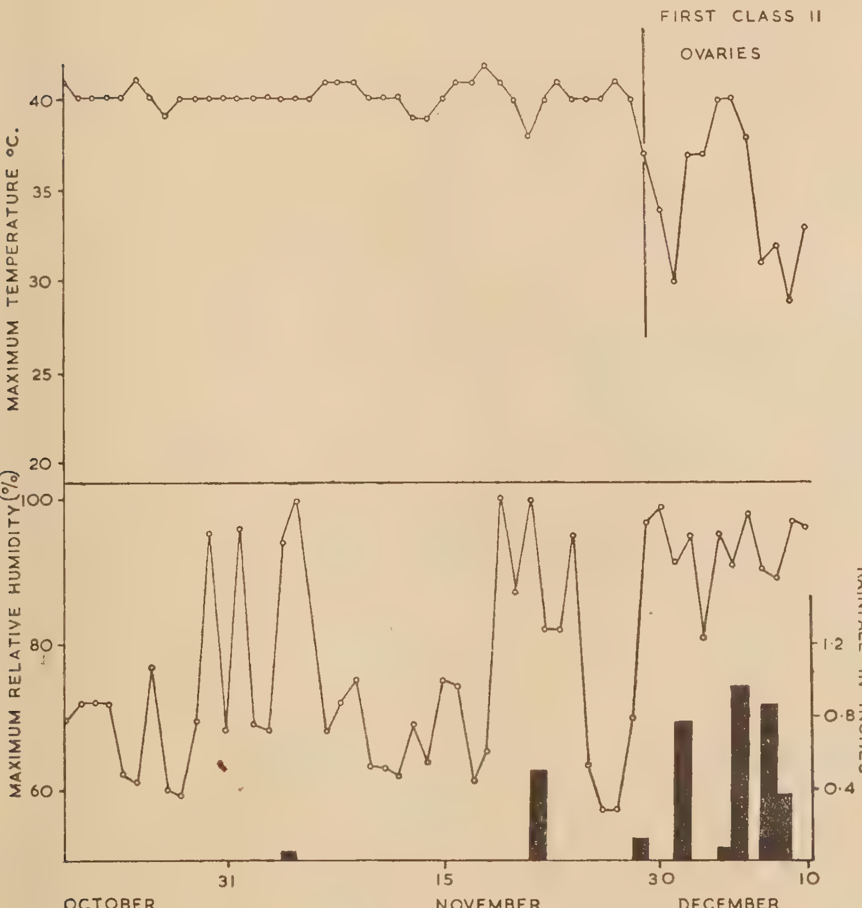


Fig. 6.—The daily maximum temperature, daily maximum relative humidity, the rainfall, and date of first appearance of Class II ovaries in 1953.

figures are studied, it appears that the date of the first rainfall is not the only, or even the most important, factor causing the initiation of egg development. The criterion used here is the first appearance of Class II ovaries (that is, ovaries containing eggs more than 2 mm. in length). It is realised that this does not in fact include the very first stage of egg development, but the rate of development from Class I to Class II is so rapid that it appears permissible to accept the

TABLE VI.

Calculated percentage increase in weight of a given size of locust during development of ovary.

Length of elytron	Class of ovary				
	I	II	III	IV	V
50 mm. %	1·28 g. 100	1·6 g. 125	1·61 g. 126	1·83 g. 143	2·01 g. 157
60 mm. %	2·3 g. 100	2·75 g. 120	3·0 g. 130	3·2 g. 139	3·5 g. 152
70 mm. %	3·3 g. 100	3·9 g. 118	4·4 g. 133	4·55 g. 138	4·95 g. 150
Average %	100	121	130	140	153

Weights of locusts given in grammes, with related increase.

In the three size groups, unity (100%) is taken as the weight of the locust with Class I ovaries.

appearance of Class II ovaries as a convenient criterion for the present purpose. In 1952, the observations were not begun until 18th November and by that date development of the ovaries had already started, so that it is not possible to make use of the data for that year. In other years, however, observations were begun several weeks before the ovaries started to develop.

In 1954 (fig. 7), the temperature began to drop from a maximum daily average of 37°C. on 3rd November. This was followed two days later by the first rains, with a big rise in the maximum daily relative humidity, and this in turn was closely followed by the first appearance of Class II ovaries on 8th November. In this case it is difficult to decide which of the factors—temperature drop, rain or high humidity—was important in initiating egg development. In 1953 (fig. 6) the first rains (0·05 in.) fell on 4th November and the maximum relative humidity rose sharply for two days. There had also been sharp rises in maximum relative humidity on 29th October and 1st November, which were probably connected with build-up of cloud cover prior to the first rains. Again, on 21st November, there was a substantial fall of 0·5 in. rain and a temporary rise in maximum relative humidity, but no Class II ovaries were found until 29th November. This was after the maximum daily temperature had begun to drop from its high average of 40°C. In this year, then, high relative humidity and a substantial 0·5 in. fall of rain in a day did not cause egg development; no development occurred until the maximum daily temperature had fallen.

In 1955 (fig. 8), the first rains fell on 17th November, but the first Class II ovaries had been found on 8th November, that is, nine days before the first rains. In this case, the first development of Class II ovaries corresponded with a sharp but temporary, increase in relative humidity. With the exception of a temporary two-day drop in temperature on 21st to 22nd November associated with the fall of the first rains but having no effect on the development of the ovaries, the maximum

daily temperature remained at an average of 37°C. until 29th November, when it began to fall. It can be seen from Table IV, however, that there was a considerable delay in egg development in 1955; it was not until 3rd December that Class II ovaries made up more than 10 per cent. of the sample, and by this time the maximum daily temperature had dropped (on 29th November) and rain had fallen on 30th November and 1st December. Humidity had also risen.

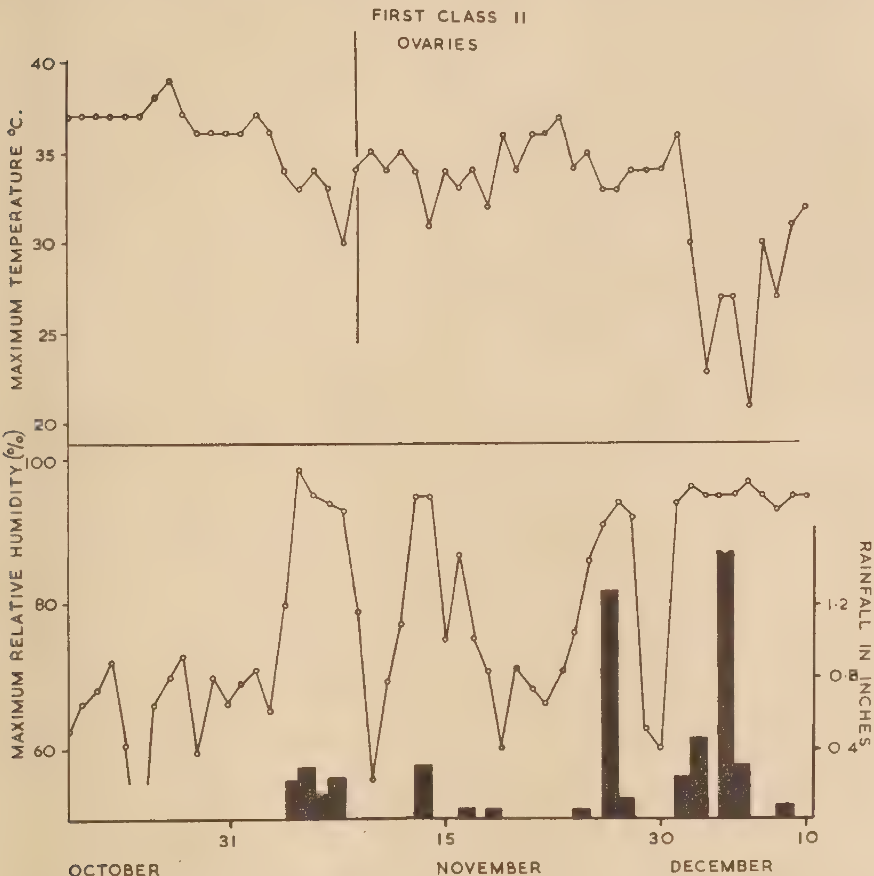


Fig. 7.—The daily maximum temperature, daily maximum relative humidity, the rainfall, and date of first appearance of Class II ovaries in 1954.

Therefore, in the three years 1953 to 1955, rapid development of the eggs did not begin until the maximum daily temperature began to fall below about 36°C., although in the different years the factors of humidity and rainfall varied considerably. The initiation of egg development would therefore seem, from the evidence of these three years, to be directly associated with a drop in maximum daily temperature, and only indirectly associated with the onset of the rains, which itself often causes a sharp drop in temperature. Thus, it appears that rain without the maximum daily temperature falling below 36°C. (1953) does not initiate egg development; such a drop in temperature, without much rain (1954) may have some initiating effect, and a sharp increase in maximum daily relative

humidity, without rain and without the average maximum daily temperature falling below 37°C. (1955), may also initiate development. However, further data are required on these points.

M. J. Norris, working on the reproduction of the Desert Locust, *Schistocerca gregaria* (Forsk.), at the Anti-Locust Research Centre, London, has found that, in the laboratory, the normal adult diapause can be broken by increasing the length of

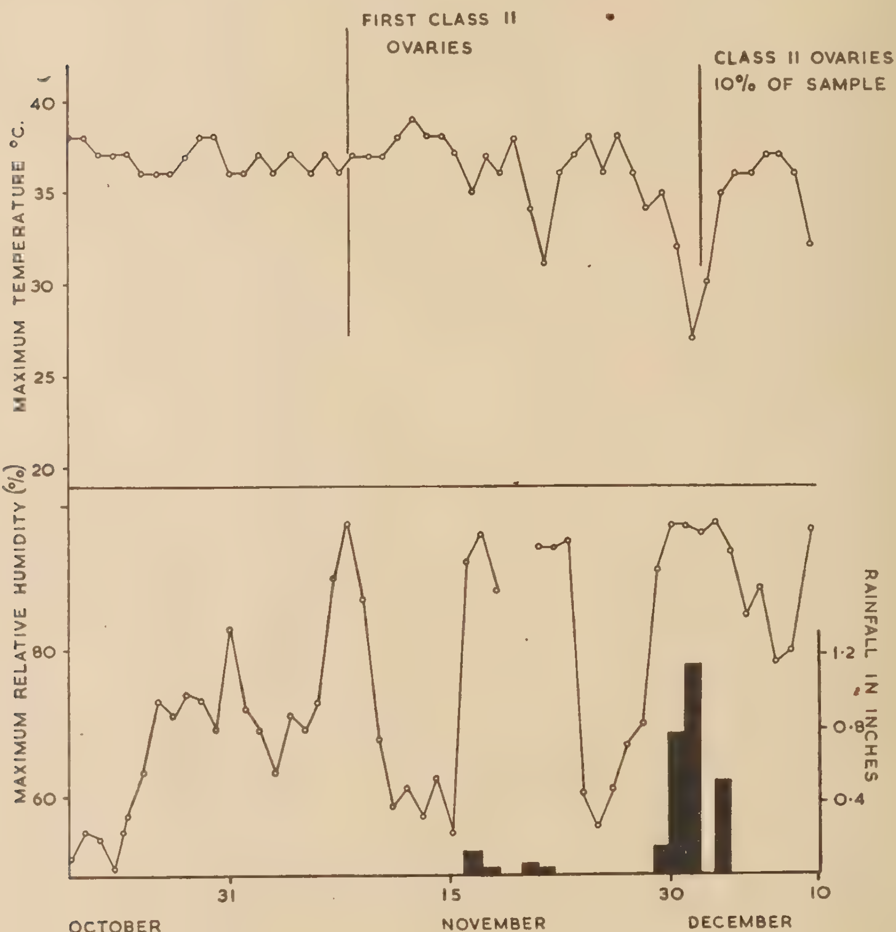
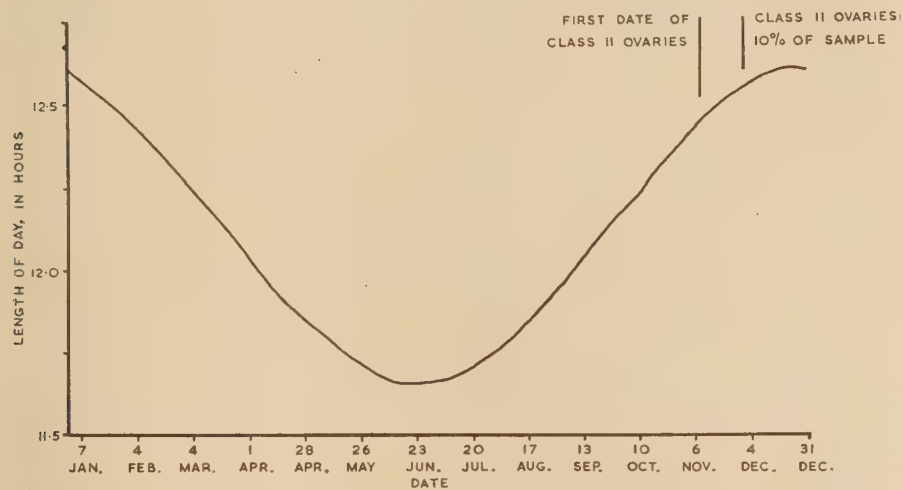


Fig. 8.—The daily maximum temperature, daily maximum relative humidity, the rainfall, and date of first appearance of Class II ovaries in 1955.

day by artificial light (Norris, 1957). Although the Rukwa Valley is near the Equator (Lat. 8° S.), the length of day (fig. 9) varies by approximately 55 minutes throughout the year. For the four years in which the observations were carried out, all egg development started between 6th November and 4th December, that is at lengths of day between 12 hr. 27 min. and 12 hr. 33 min., near the end of the period of increase. The other dates when the day is as long or longer follow on until early February, which is the period of egg-laying. The first new adults

generally appear in mid-February, when the days are shortening and are already reduced to 12 hr. 20 min., reaching a minimum of 11 hr. 40 min. in June. That is to say, although the period of eight months of adult diapause in the Red Locust does correspond largely with the dry season, it may be that, in the field as in the laboratory, short days are a factor in the diapause. It may be thought that the changes in the length of day are too slight to have much effect, but it has been shown by Lees (1955) that small changes in length of day may have a critical effect on insect physiology. The situation is complicated, however, by the fact that Albrecht (1953) succeeded in breaking the adult diapause in open-air cages by conditions of high humidity alone. Starting at the normal time of breeding, he obtained his second generation in July, in the period of short length of day. Therefore, it would seem that although diapause may be broken by single factors in the laboratory or in cages, in the field it is controlled by several factors.



TIME OF:														
SUNRISE	5.48	6.00	6.04	6.02	6.02	6.05	6.11	6.15	6.09	5.55	5.40	5.31	5:33	5.44
SUNSET	18.22	18.27	18.18	18.04	17.53	17.48	17.51	17.57	18.00	17.57	17.54	17.56	18.06	18.19

Fig. 9.—The change in length of day at the latitude of the Rukwa Valley throughout the year, showing the local times of sunrise and sunset. (Based on data in the Nautical Almanac for 1955.)

Although the figures quoted above are from the Nautical Almanac for 1955 (1954), it should be realised that these times of length of day, being calculated from sunrise to sunset, may not be applicable to the whole of the Rukwa Valley. In places, the western escarpment rises sharply to a height of 3,000 ft. above the Valley floor, so that the nearest locust breeding places, four miles away, are shadowed more than half an hour before sunset; indeed, the Valley is only about 30 miles wide, so that even the eastern side loses a few minutes of late sunshine. In other areas there is no such effect. The quality of the light involved in breaking diapause also needs investigation, especially in relation to the prolonged twilight experienced near the western escarpment.

This restricted November to January breeding season of the Red Locust is not typical of all the Acrididae of the Rukwa. The majority of the species lay eggs at the beginning of the rainy season, but many do not. *Cyrtacanthacris*

aeruginosa aeruginosa (Stoll), a large Catantopine grasshopper, lays eggs from March to May, when the length of day is decreasing rapidly. Another species, *Tylotropidius speciosus* (Wlk.) lays eggs in September and October, under a regime of increasing, but still shortened, length of day.

Factors Affecting Egg-laying.

From Table VII, which was compiled from the data obtained on the percentages of locusts with Class V ovaries, and the dates of the decline in population numbers (figs. 1–4 and pp. 493–494), it will be seen that there was a very considerable difference in the numbers of egg-pods per female laid in the four years. It will also be noted that there were similarities between 1952 and 1954 and between 1953 and 1955, both in the dates of first egg-laying and in the numbers of egg-pods.

In 1954, the drop in maximum daily temperature took place on 3rd November (fig. 7). Also, in 1952 the drop in maximum daily temperature took place on 3rd November. In 1953 and 1955 (figs. 6 & 8) the drop in temperature was later, occurring on 29th and 28th November, respectively. Therefore the main difference between 1952 and 1954, on the one hand, and 1953 and 1955, on the other,

TABLE VII.

Approximate percentage of population laying various numbers of egg-pods, 1952–53 to 1955–56.

Year	Date of first laying	1st pod	2nd pod	3rd pod	4th pod	5th pod
1952–1953	28/xi	100	100	20	5	—
1953–1954	12/xii	60	7	—	—	—
1954–1955	19/xi	100	100	50	50	5
1955–1956	8/xii	70	20	2	—	—

was in the date of the drop in maximum daily temperature. The date on which the first egg-pod is laid appears, therefore, to be correlated with the date of the drop in maximum temperature, which supports the conclusion, drawn from the data (figs. 6–8) on development of the ovaries, that the latter does not begin until the maximum daily temperature has fallen below 36°C.

Again, in both 1952–53 and 1954–55 (figs. 1 & 3), the decline in population occurred at a much later date than in 1953–54 and 1955–56. In 1952–53, the population remained at its original level until 30th December and fell sharply to less than 50 per cent. of that level by 2nd January, and in 1954–55, although it began to decline about 7th December, the decrease was gradual and approximately 50 per cent. of the population was still alive on 3rd–5th January. In 1953–54 and 1955–56, the 50 per cent. level was reached about 11th–15th December and 7th–13th December, respectively, and by 30th December only a very small percentage of the original population was left alive (figs. 2 & 4).

The limiting factors affecting egg-laying are, therefore, the date of the drop in maximum daily temperature and the date of the drop in adult population. In both 1953 and 1955, when the temperature drop was late, the drop in adult population was early, so that the period available for egg-laying was reduced at both ends. It is considered that a likely reason for this double check would be that the parental population had to withstand a more severe dry season than

usual. The period before the onset of the rains and the drop in temperature is the hottest of the year, and the vegetation is dry and unpalatable, so that, if the change was very late, the vitality of the parental population might be reduced, causing the production of fewer egg-pods and early death. Therefore, although a parental population may be large, it does not follow that the succeeding generation will also be large.

Factors limiting Egg Production.

In the past, a considerable amount of work has been done on the fecundity of locusts, mostly in the laboratory, and mainly on *Locusta migratoria migratorioides* (R. & F.) and *Schistocerca gregaria*. Most of the work on *Nomadacris* was done in the middle 1930's, when the last plague was at its height. Mossop (1933), Lea & McMartin (1934), and Smee (1936) all suggest that females lay 2 or 3 egg-pods. Faure (1935) in South Africa mentions two experiments in which mature females were caught in the field and placed in cages; six females laid 4 pods each, 11 laid 3 each, and 17 laid 2 each, the average interval between successive layings being 15 days. Smit (*in* Faure, 1935) found that, in cages, 18 females averaged 2·6 pods, the maximum number laid by one being 5; the average interval between layings was 14 days. Hamilton (1936), in cage experiments under controlled laboratory conditions, obtained a mean figure of 0·98 pods per female. Johnston & Buxton (1949) in Uganda found that, in cages, four females laid 2 pods each, the layings being at intervals of 19 days, and two laid one each. Burnett (1951), working with caged locusts in central Rukwa, obtained an average of 2·2 pods per female, the interval between layings being 19 days or less. Albrecht (1953), also working with caged locusts in central Rukwa, recorded the same average of 2·2 pods per female.

Thus, all these authors, except Hamilton (1936), agree that the Red Locust lays more than one egg-pod, and those who have also dealt with the number of days between successive ovipositions by an individual, give periods varying from 14 to 19 days. From the peaks on figs. 1–4 it will be seen that the present results fall within these limits, the average being 16·2 days.

In the Rukwa Valley, the rainfall varies considerably from year to year (figs. 1–4). In 1953–54, 1954–55 and 1955–56 the rainfall was well distributed, and it is not considered that it had any appreciable effect on egg development. In 1952–53, however, the rainfall record shows a drought, after the first peak of Class V ovaries, from 8th–31st December, during which time the average daily maximum temperature was 35°C. The graph of the percentage of locusts with Class V ovaries (fig. 1) suggests that the locusts were compelled to postpone laying by lack of suitable damp soil. The extended peak of Class V ovaries on the graph, from 9th–17th December, indicates that the eggs were retained for eight days, but were then laid, although the soil conditions still seemed to be unsuitable. There may be two explanations for this: the locusts may have been physiologically incapable of retaining the eggs longer, or increasing relative humidity before rain actually fell may have affected oviposition. There is no direct evidence for either supposition, but it is considered that the former is the more likely.

The Figures and Table VII show that both the level of population and the date of laying vary considerably from year to year. If both features are considered together, some idea of the success of laying will be obtained. In 1952–53, the peaks of Class V ovaries occurred on 28th November and 9th–17th December, with a suggestion of a third peak on 9th January. Relating these dates to the population, it will be seen that, as the drop in population did not take place until 30th December, most, if not all, of the females laid two egg-pods, while in January only some 20 per cent. remained to lay a third. A very small percentage, about 5 per cent., would have survived to lay a fourth pod. In 1953–54,

the decline in population began very early, and this was associated with late commencement of laying. From the evidence, it seems that some females died before any layings took place, so that only 60 per cent. laid (on 12th December) and only about 7 per cent. survived to lay a second pod (28th December). In 1954–55, the population is considered to have remained constant until 7th December, confirmation of this date having been obtained independently from the results of intensive scouting over an area of 24 sq. miles in central Rukwa, and by that time two layings had taken place. Some 50 per cent. then survived to lay third (23rd December) and fourth (3rd–5th January) pods, while 5 per cent. probably survived to lay a fifth. In 1955–56, as in 1953–54, the population decline began very early, and again it seems that some of the females died before the first layings took place on 8th December. Thus it is estimated that some 70 per cent. laid a first egg-pod (7th–8th December), while only 20 per cent. survived to lay a second (27th December) and some 2 per cent. to lay a third.

In 1952–53, the laying was quite successful in spite of the long drought. Hatching, however, was severely affected (Albrecht, 1956), with the result that the adult population in 1953 was very low. In 1953–54, the rains seemed to be satisfactory, yet reproduction was very unsuccessful, both in number of pods laid and in number of eggs per pod (Robertson, 1954). Nevertheless, in spite of the small parental population of 1953 and the subsequent poor breeding, the population of 1954 was at least five times as great and, although control measures were undertaken, a considerable breeding population was present in November. In the breeding season 1954–55, the rains were again good and, as shown above, egg-laying was very successful. This resulted in a large adult population tending to form swarms, and control work was necessary. In 1955, in spite of control measures, a considerable parental population was present when the rains began, and the rains seemed to be satisfactory; nevertheless, laying was unsuccessful, and in 1956 no control operations against adults were necessary in or near the experimental area.

In a previous paper dealing with the number of eggs in egg-pods of the Red Locust (Robertson, 1954), it was stated that, from earlier evidence together with the work described, it could be estimated that a Red Locust population was capable of increasing 100-fold in a single year, assuming a sex ratio of unity and that the average number of eggs per pod is 90. The present work, over the period 1952–53 to 1955–56, confirms that this supposition is reasonable, the average number of egg-pods laid per female being 1·7.

Summary.

During the breeding seasons 1952 to 1955, samples of females of the Red Locust, *Nomadacris septemfasciata* (Serv.), were caught in the Rukwa Valley, Tanganyika Territory, and the ovaries classified according to egg length. Ovaries designated Class V were those regarded as containing eggs ready for oviposition. Population estimates and rainfall records were also taken.

The data suggested that the eggs in the ovaries develop very rapidly, becoming ready to be laid about seven days after the start of development.

The increase in weight of an individual female during ovary development is related to absolute size, and it was found that, during ovary development, the weight increases by approximately one-half.

The most important factor initiating ovarian development seemed to be a drop in daily maximum temperature to below 36°C. The factors of high humidity and rainfall were of less importance but their influence is not fully understood. The possibility of change in length of day being an important factor in the initiation of ovarian development is discussed.

The limiting factors for the number of egg-pods laid in a season are considered to be the dates of the drop in daily maximum temperature and of the

drop or decline in parental population. The date of drop or decline in parental population seemed to be connected with the date of drop in daily maximum temperature.

The percentage of females laying more than one egg-pod was calculated, and the results were found to vary considerably from year to year, although the average of 1·7 pods per female agreed with past estimates. Also, the average period of 16 days between successive egg-layings agreed with past work.

Drought, during the laying period, seemed to cause the females to retain their ripe eggs.

The evidence tended to confirm the possibility of a Red Locust population being able to increase 100-fold in a single year.

Acknowledgements.

I wish to thank Dr. D. L. Gunn, Director of the International Red Locust Control Service, for his help in the preparation of this paper; Mr. J. G. Skellam, Nature Conservancy, London, for his very kind assistance with the statistical analysis; and Dr. F. O. Albrecht, who initiated the work.

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AN EXPERIMENTAL CAMPAIGN WITH LIGHT AIRCRAFT AGAINST FLYING LOCUST SWARMS IN NEW SOUTH WALES.

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(Plate XVII.)

Recent experience in the use of aircraft against adults of the Desert Locust, *Schistocerca gregaria* (Forsk.), in India (Pruthi & Bhatia, 1953) and in Kenya (Rainey & Sayer, 1953) and against the Red Locust, *Nomadacris septemfasciata* (Serv.), in Tanganyika (Gunn & others, 1948) has emphasised the important part aircraft can play in a locust control campaign. The limitations of aircraft spraying techniques that are dependent on ground parties for scouting and demarcation are also indicated. In Australia, aerial techniques have been investigated by the Department of Agriculture of Victoria during 1945–48 (Hogan, 1949, 1951). Campaigns were also carried out by that Department in 1946, 1950 and 1953 using Dakota aircraft (Hogan, 1955). Experience with the use of large Dakota aircraft by the N.S.W. Department of Agriculture in 1953, however, indicated many associated problems of organisation and it was considered that light aircraft requiring a much reduced ground organisation might prove more suitable for the treatment of adult locust swarms.

In the autumn * of 1955, large and extensive flying swarms of the Australian Plague Locust, *Chortoicetes terminifera* (Wlk.), invaded wide areas of south-west New South Wales, Victoria and South Australia. These swarms apparently originated in or near the inland breeding areas mapped by Key (1945) and moved south into the agricultural districts of New South Wales, Victoria and South Australia. Egg-laying was particularly heavy in south-western districts of New South Wales and much of this area is typified by flat, treeless plains traversed by a few rivers and creeks of the Murray River system. Properties are large, settlements scattered and available manpower limited, making the consequent task of controlling resultant spring * hatchings difficult.

The present paper describes a campaign carried out by the New South Wales Department of Agriculture with light aircraft (Tiger Moths) in November–December 1955 to prevent large adult swarms of locusts invading rich farming lands of the Murrumbidgee Irrigation Area which lie to the east and south of the above districts and which are in the line of flight of locust swarms that develop in those districts in November and December. Supplementary trials carried out approximately 150 miles further south are also described.

Preliminary Trials.

As there was no previous record of light aircraft having been used for the control of flying swarms in Australia, preliminary trials were carried out in the Ivanhoe district where hopper swarms were just reaching the winged stage.

Tiger Moth aircraft equipped with a standard spray boom running beneath the wings were hired with pilots and ground crew from a commercial agricultural firm. The total length of boom was approximately 10 yards and it was fitted

* The Australian seasons are as follows: spring—September, October, November; summer—December, January, February; autumn—March, April, May; winter—June, July, August.

with nozzles, the number of which could be altered to adjust the output per acre. The front cockpit had been converted into a tank of 50 gallons capacity. Liquid was pumped from the tank through the boom nozzles at a pressure of 20 lb. per square inch, the pump being operated by a wind-driven fan. Operating speed of the aircraft was about 70 m.p.h.

Three experimental treatments were carried out in the Ivanhoe area after suitable swarms had been located by scouting truck or local report the day before spraying was to take place. An observer remained with the swarm selected until after sunset and roughly defined the swarm limits. He also located a suitable landing strip. It was essential that the strip should be not more than five miles from the treatment area. The distance needed for take-off (fully loaded) was 300–400 yards of fairly level ground without trees at either end. On this flat, plains country this requirement was easily met.

Ground parties proceeded to the selected area before dawn on the following morning, when it was often found that the swarm had moved slightly, especially after a warm night. Time was often wasted finding the swarm and re-defining its boundaries. In warm weather, the locusts tended to move off by about 9 a.m. and the time thus available for treatment was often very limited. Difficulty was also experienced in placing ground markers to the greatest advantage due to the complex nature of the swarms and it was sometimes necessary to spray areas where there were few or no locusts. The terrain was often rough, being heavy black soil with grass cover and concealed depressions. The spray runs were generally short and the turning circle of the Tiger Moth was so small that men with flags acting as markers often had difficulty in maintaining contact with the spraying aircraft.

Microscope slides, coated with magnesium oxide, and tissue paper strips were used to determine the swathe width in relation to droplet size and concentration. Early tests revealed that the low-flying technique with precise, narrow swathe widths used for crop spraying was totally unsuitable for locust spraying. Spraying height was increased so that larger droplets fell 15 yards either side of the plane path while fine droplets fell out for 80–100 yards downwind of the aircraft with good concentration of small droplets for 50–70 yards. In order to obtain a reasonable ground cover, swathes of this type should clearly be overlapped. Instruments were not available for measurement of wind speed or aircraft height and reliance was placed on estimations by the pilots who were considerably skilled in this aspect. It was finally decided to make spray runs 50 yards apart which, with the full complement of 16 nozzles, gave an application rate of one gallon per acre and one plane load was thus designed to cover 50 acres adequately with a considerable drift of smaller droplets outside this area.

The insecticide used was an emulsifiable concentrate containing 7 per cent. γ BHC, diluted with diesel oil. The dosage rate in the early trials was $2\frac{1}{2}$ pints of the concentrate per acre, equivalent to 3·5 oz. of γ isomer. This was later increased to 5·6 oz. of γ isomer per acre as the spraying technique was developed.

It was felt at this stage that, although it was possible to treat settled swarms early in the morning, a much larger organisation than the one available would have been necessary to carry out a large project successfully. Restriction of the spraying aircraft to ground markers and to the early hours of the morning severely limited the mobility of the whole unit. Consequently, the pilots were instructed to attempt spraying without markers, making their runs 50 yards apart across wind. This proved impossible with resting swarms but, when locusts were in the air, the pilot was able to use the swarm itself to judge the spraying intervals. The sound of the aircraft engine passing overhead or the contact of insecticide caused the locust swarm to rise into the air and this aided accurate placement of the spray.

The preliminary results were so encouraging that a complete change of tactics

was planned and the final method chosen represented a gradual progression from the precise spraying at low heights and resultant narrow swathe widths to a greater use of wind drift, and a lower gallonage, with correspondingly higher insecticide concentration, per acre. Ground markers were dispensed with and the treatment was directed against flying rather than settled swarms.

The aircraft were found useful for scouting and spotting, and many swarms were actually located in this way on warm days when many locusts were in the air. Several large swarms were tracked day after day and this allowed the unit to keep well ahead of advancing swarms.

Terrain and Locust Behaviour.

The region where spraying took place consists mainly of open grassland (see Pl. XVII, fig. 1) or saltbush plains traversed by the Willandra and Merrowie creeks and the Lachlan river north and west of the town of Hillston. Locust swarms moving south across the plains tend to mass along the timber lines of these creeks, often for several days, and it is here that they are most readily treated.

To the east of Hillston, areas of mallee scrub (*Eucalyptus oleosa–E. dumosa* association), belah and rosewood scrub (*Casuarina–Heterodendron* association), bimble box and pine woodland (*E. populifolia–Callitris glauca* association) (Beadle, 1948), and the rough Lachlan Range district tend to restrict any easterly movement of swarms. These natural barriers also direct locust swarms in their general south-easterly movement. Major swarms follow regular "driftways" and the appearance of swarms at certain points can often be predicted during an infestation. Some properties and particular spots on creeks are notorious for the regularity with which swarms appear in plague years. Flying swarms moving across open plains are temporarily baulked by timber belts along creeks and rivers. Although quite capable of flying over such narrow timber lines the locusts appear unwilling to do so and will often travel slowly up or downstream until a gap in the timber is found. However, when travelling through well timbered country the swarms tend to drift through without pause and are often difficult to locate and treat.

Spraying was later carried out in the Jerilderie district 150 miles south of Hillston. This area is similar to the Hillston district, being composed of flat, grassland plains traversed by the Billabong and Yanco creeks, each with a narrow timber fringe. A map (fig. 1) shows both areas.

Two types of travelling swarm, high-flying and the so-called rolling swarms have been recorded. The former, which travel day and night and upwards of 100 miles per day, are rare and none was observed during the whole campaign. Rolling swarms represented the major part of those seen and they consisted of many locusts on the ground as well as in the air at any one particular time. There was a constant interchange of settling locusts and locusts leaving the ground so that the swarm as a whole moved forward relatively slowly, often in the general direction of the prevailing wind. Swarms could often be seen as a brownish-coloured haze on the horizon, the locusts being occasionally up to several hundreds of feet in the air but generally not more than 50–100 ft. The rate of travel of individual locusts was observed to be 7–10 m.p.h. but the speed of the swarm as a unit did not exceed 5 m.p.h. and was usually somewhat less. Little swarm movement was observed on cold or windy days.

Rolling swarms gathered up loose, small swarms of locusts as they travelled and gradually increased in size and density. Loose and scattered, small swarms of locusts could be found over many square miles of the infestation area during the campaign but attacks were directed only against the dense centres of swarms and scattered fliers were not treated. Light aircraft with small loads appeared to be unsuitable for the treatment of loose, small swarms of scattered locusts over a wide area.

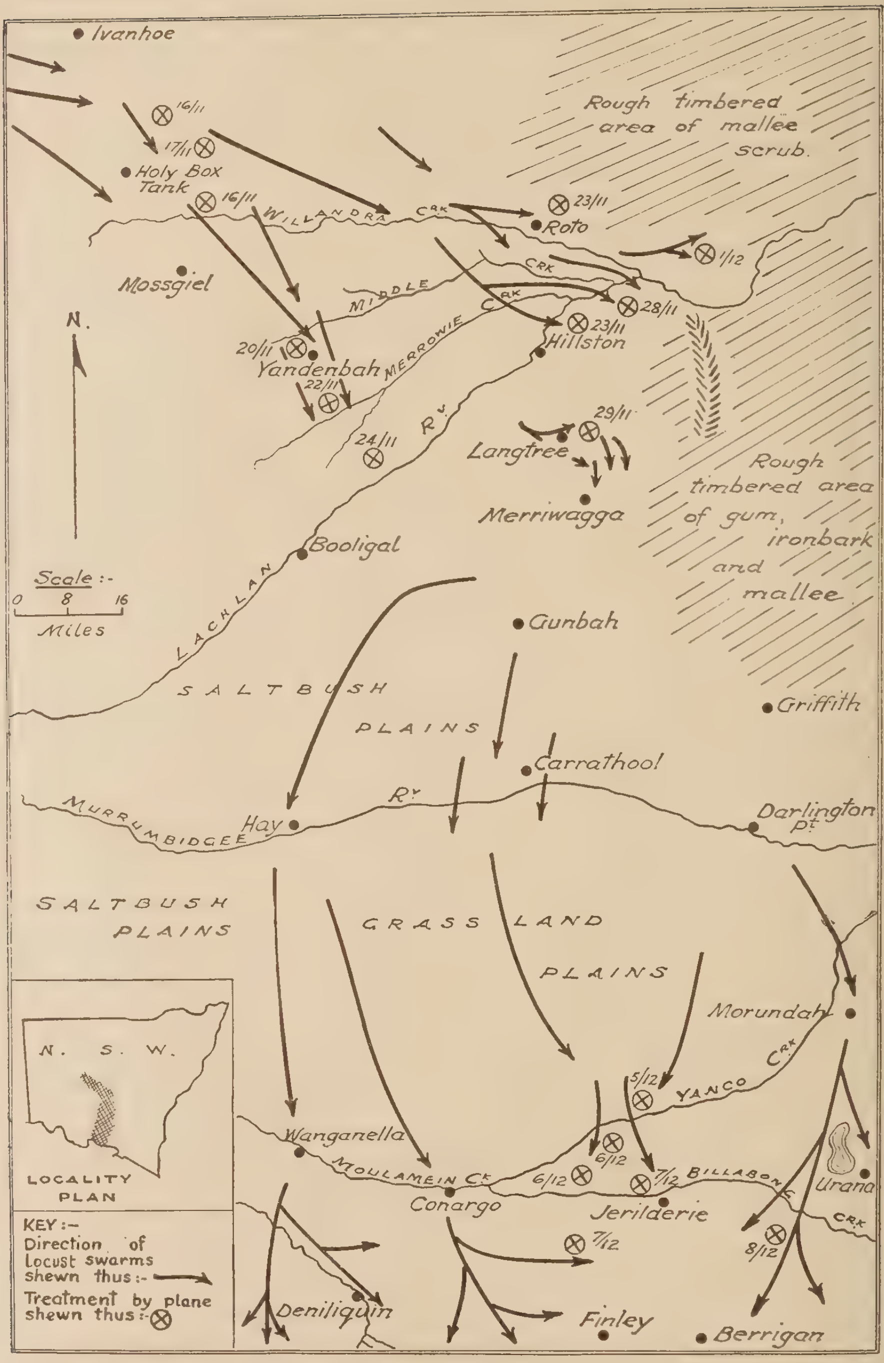

Fig. 1.—The areas in Hillston and Jerilderie districts where aerial spraying was carried out.

Locust Spraying Operations.

As already indicated, spraying operations were carried out in two distinct parts of the infestation area. The first, the Lachlan river area, represented a transition from flat grassland plains to closer settled districts further south and east, and the town of Hillston on the Lachlan river was chosen as a suitable base of operations, being, at that time, well south of invading locust swarms. Eleven separate operations were carried out in this area from 16th November to 1st December, six being against large and dense travelling swarms.

After completion of spraying in the Lachlan river area a move was made to the second base of operations, about 150 miles to the south, where several large swarms had appeared on 6th December and were temporarily halted by the narrow timber fringe on the Yanco creek. By 8th December all swarms had crossed the creek, some flying all night. They moved quickly into irrigated and timbered districts further south and then dispersed as loose swarms over a wide area, the only aggregations occurring on areas of succulent green feed. Five separate spraying operations were carried out in this area and, as it was not considered feasible to treat scattered swarms with the light aircraft available, control was not attempted after the swarms had dispersed. The location and dates of the various treatments in both areas are indicated in fig. 1.

Two Tiger Moth aircraft were operated with a team of the two pilots, an engineer and an assistant. One entomologist directed and supervised the actual spraying, another was responsible for checking and appraising swarms, whilst a field officer organised and channelled information on locust movements, and arranged insecticide supplies. A large semi-trailer transport vehicle was hired to carry insecticide to the treatment area. Sixty eight 45-gallon drums could be carried on the semi-trailer, 34 drums of insecticide concentrate and 34 of diesel oil, this being sufficient for a full day's work with two aircraft.

When a suitable swarm was located, the ground crew and entomologists proceeded by truck to the area early in the morning and chose a suitable landing strip nearby. The aircraft arrived later at the swarm area determined and in the event of swarm movement kept contact with the locusts and sometimes selected a more suitable landing strip.

Equal parts of insecticide concentrate and diesel oil were pumped directly from the drums on the semi-trailer into similar empty drums on the ground nearby, each drum of mixture making a single load for one aircraft and being sufficient to treat 45 acres of swarm at the required rate of 5·6 oz. of γ BHC per acre. The total loading time, from the moment of landing to the take-off again, was two minutes, and under favourable conditions 6–8 loads per hour could be delivered by each plane.

The success of the campaign rested on the ability of the party to locate and keep track of all major swarms in the area. Publicity was given by local radio and newspapers and landowners were contacted personally. Information was telephoned to a central depot and a constant stream of information was received, although much of it was inaccurate and one of the entomologists was fully occupied in checking reports by truck and locating suitable swarms for treatment.

In all, 16 spraying operations were carried out and two of these are described in detail below. The locust swarms involved were among the largest encountered and the treatment procedures were characteristic of the method used on all occasions.

Operation A.

A swarm, 35 miles west of the town of Hillston, was surveyed on 19th November and found to be 3 miles long and ½ mile deep and settled densely in open grassland. The following day this swarm was joined by several other rolling swarms moving south from the Willandra creek. They were travelling

across a slight breeze in a south or south-easterly direction and were up to 100 ft. in the air but mainly at 0–20 ft. The total area covered by these aggregated swarms was 6–7 square miles and 70–100 locusts per square yard were counted in a dense swarm when they had temporarily settled. The various aggregations were connected by thin streams of flying locusts.

Spraying commenced at 12 noon and finished at 5.30 p.m. and it represented the first real test of the method. A total of 20 loads (900 gallons) was applied from one Tiger Moth. The landing strip selected was strategically placed in the line of flight of oncoming swarms and the aircraft never travelled more than 3 miles to release spray.

At first, long spraying runs (2½ miles) were attempted across the entire face of the main swarm but this proved unsatisfactory and later spraying was directed along a small belt of timber where swarms tended to mass (Pl. XVII, fig. 2), and several short runs were made over the densest portion of the swarm. It was found that the spacing of the runs was not particularly important as long as each was applied to the densest portion of the swarm, and, apart from keeping in mind the approximate 50-yard interval between spray runs, strict adherence to a precise swathe width was not maintained. The pilot endeavoured to make maximum use of spray drift, which was 80–100 yards. Depending on the wind speed and the height at which locusts were flying, the aircraft operated at from 50–100 ft. to achieve this drift. Several swarms, or rather several parts of the one complex swarm, passed over this restricted area, each pausing at the tree-line, and they were sprayed as they arrived.

Locusts were observed falling out of the air ½–1 minute after spraying and many were still being affected hours afterwards. Repeated spraying tended to break up the swarms, and locusts not directly hit by the spray often settled or milled around in the sprayed area. Further residual kills were thus obtained on settled and feeding locusts. Counts of dead locusts were made the day after spraying although ants, birds and weather had removed much of the evidence, portions of locust wings and legs being observed over a wide area in great profusion. Fifteen counts in the treated area averaged 25 dead per square yard with some still dying. At points ¾ mile downwind from this area the figure was 5 per square yard while 1½ miles away the average was one per square yard. No dead locusts were seen at points 3½ miles and 4½ miles downwind in a heavily grassed area although individuals obviously affected by insecticide were observed. It was thought that a considerable part of the swarm complex had been killed but that part had escaped treatment and moved south.

Intensive ground search on 21st November showed that two or three dense sections of the swarm had escaped and moved on to a heavily grassed area on the north side of the Merrowie creek 10 miles to the south and were feeding extensively. One swarm was massed against the tree line in a bend of the creek. Swarms were not as extensive as expected but were very dense and were either feeding or moving slowly along timber on the creek. The day was warm and cloudless with a breeze of 5–10 m.p.h.

A total of 12 loads (540 gallons) was applied on 22nd November, 8 on swarms along the timber, 3 on a swarm 2–3 miles from the creek, and 1 finally on the creek as more locusts drifted into the area. Dense patches in bends of the creek were sprayed first, then the moderately dense swarm on the plains to the north, so that survivors (and probably some affected locusts) flew into the creek area. One plane load along the timber was then sufficient to deal with the last accumulation of locusts.

Only scattered locusts were visible in the area after spraying ceased. Reports from landholders in the area stated that locusts were still dying 3–4 days later and that there was no build-up of further swarms. A few scattered locusts crossed the Merrowie creek to the south but a close watch on the general area

for one week revealed no significant swarms and it was considered that the swarm complex had been eliminated by the two days of spraying.

Operation B.

The second operation to be described in detail was one of those carried out in the Jerilderie district. After three days of rain a large swarm was located on 5th December, settled in long grass on the northern bank of the Yanco creek. The day was cool, with broken cloud and a strong breeze, but conditions gradually improved during the day. Locusts were commencing to move in the warmer, calm spells. The area involved was 8 × 3 miles, occupied by several dense aggregations which had remained separate in the cool weather.

A total of 42 plane loads (1,890 gallons) was used by the two aircraft, both pilots working without assistance from ground markers. The aircraft also carried out their own scouting and worked separately on different parts of the swarm. An area of 5–7 square miles of dense swarm was treated. Under the cool conditions prevailing, the locusts, disturbed by the roar of the aircraft engine, tended to settle almost immediately this had faded away, but were quickly flushed up when contacted by the insecticide. Both pilots were very accurate in their spray runs despite the difficult conditions.

Large numbers of dead locusts were not observed soon after spraying as is usual but many were obviously affected in all treated areas some hours after spraying. During the day the swarms gradually thinned until only scattered individuals remained. Extensive scouting revealed no escape of locusts from the treated area and an excellent kill had apparently been obtained.

This area represented approximately the eastern half of a large swarm reported to measure 15 × 3 miles. It was intended to treat the remaining portion on the northern side of the creek but on the morning of 6th December the locusts had moved south. They had also been reinforced by swarms moving in from the north. The main bulk of the swarm was located along the timber line on the south side of the Yanco creek. It was six miles long and one mile wide and was visible for miles as a brown cloud hanging in the air. It was the biggest single aggregation seen during the campaign. Several dense patches were also present along the timber line of the Billabong creek, three miles south of the main swarm. A constant stream of locusts was travelling south and south-west between the two aggregations and they were up to 200 ft. in the air on a 3–4 mile front.

A good landing strip was found between the two groups of locusts, directly in their line of flight. One aircraft operated on the swarm while the other had a roving commission to treat all dense patches along the Billabong creek and elsewhere. A total of 60 loads (2,700 gallons) was used and an area of 8–10 square miles treated. When hit by the spray, locusts in the main swarm rose in clouds to a height of about 500 ft. The aircraft operated from heights of 100–300 ft. and a spray drift of up to 200 yards was obtained.

By the end of the day only loose groups of locusts remained in the main swarm areas. During spraying operations, constant streams of locusts were observed flying south from the main swarm into the area being treated by the second aircraft. Counts of 8–20 dead per square yard were made over a wide area in the vicinity of the main swarm. Dead and dying at 8–10 per square yard were also observed late in the day south of Billabong creek, three miles from the nearest sprayed area.

It was thought that a full day's spraying on 7th December might be needed in the vicinity of the main swarm to complete control of the swarms. However, the number of locusts remaining was many less than expected.

A total of 12 loads (540 gallons) was released on small but dense patches of locusts in timber along the creek on 7th December. Scattered locusts filtered

into the area all day and settled on treated grassland. These areas were probably considerably overdosed. By midday there were not sufficient locusts to treat and it was considered that the major part of the swarm treated the day before had been wiped out.

Extensive scouting by air revealed only a few dense patches of locusts on crops and lucerne paddocks to the south-west and 8 loads (360 gallons) were released on them. The aircraft travelled up to 15 miles to treat these locusts, which were considered to be a residue of a large swarm (untreated) that had moved south-east from a point 30 miles to the west.

Quantities of Insecticide used and Costs of Campaign.

The amounts of insecticide used and the number of plane loads applied are given in Table I for each of the districts in which the aircraft were operated. Costs of the campaign can be calculated approximately, the major items being the hire of the aircraft and crew and of the large semi-trailer vehicle for transport of material, and the cost of the insecticide itself and the diesel oil diluent. Several smaller, incidental charges have been omitted in the calculations summarised in Table I.

The total area of swarms treated is most difficult to estimate accurately in view of the flexible nature of the spraying method and the complex structure of many of the swarms treated. One gallon of liquid was designed to cover an acre of swarm and at this rate about 5,000 acres would have been treated in the Hillston district and 8,000 acres in the Jerilderie district. The observed size of all the swarms treated would give figures almost double these and it is considered that, as the campaign progressed, effective use of the spray was obtained at much less than one gallon per acre. Thus a rough estimate of the area of swarms treated is 10–12 square miles for the Hillston district and 20–25 square miles for the Jerilderie district.

TABLE I.

	Ivanhoe	Hillston	Jerilderie	Total
Number of plane loads	8½	87	159	254½
Gallons of spray (BHC-diesel oil) ..	383	3915	7155	11453
Gallons of 7 per cent. γ BHC concentrate	150	1957	3420	5527
Cost per plane load	£44.5.0	£54.15.0	£54.0.0	—
Total cost	£376	£4,763	£8,586	£13,725
Area of locust swarms	10–12 sq. miles		20–25 sq. miles	30–37 sq. miles
Cost per acre of swarm	13—16/-		11—13/-	11—16/-

On this basis, estimates of the cost of treatment per acre of locust swarm are given in Table I. It should be remembered that they are based only on the approximations outlined above and must therefore be regarded as highly tentative.

Discussion.

The questions whether the destruction of adult swarms of the Australian Plague Locust by spraying from small aircraft would be effective and economical,

and secondly, whether the aircraft could carry out a complete protective campaign, were answered by the successful results of the campaign in the Hillston district, although operations were on a relatively small scale. However, later spraying operations in the Jerilderie district did prove the ability of light aircraft to tackle very large swarms, up to 6 sq. miles in extent, and also revealed some of the limitations of this type of treatment.

As is usual in such campaigns, the time available for subsequent investigations of the effects of the various treatments was limited. Nevertheless, the observations made do indicate that all swarms treated in the Hillston district were broken up by the spraying aircraft and, in some cases, were practically eliminated. In every instance, the large, coherent aggregations of locusts were reduced to scattered populations. Extensive scouting by air and by truck revealed no significant escape of locusts from the treated areas and, where it was possible for observations to be continued for some days after spraying, no regrouping of survivors was observed. Only two of the largest swarms required more than one full day's treatment to achieve satisfactory control. However, in the absence of an accurate and thorough method for the assessment of mortality, the main criterion for the success of the campaign in the Hillston district was the fact that no swarms crossed the Lachlan river to invade the farming areas further south. Reports continued to be received from Hillston for some weeks after the aircraft had left the district and no swarms were observed anywhere along the river during December. The type and number of swarms observed during the campaign and experience during a similar plague in 1953 left no doubt that, had treatment not been carried out, the locusts would have invaded the more closely settled districts south of the Lachlan river and also reinforced the large breeding population of locusts in this area. The rolling swarms tend to gather in size and momentum as they travel by picking up loose, small swarms and scattered locusts and much of the area south of the Lachlan river supported such scattered, small swarms.

The most suitable method of treatment for the types of rolling swarms encountered was found to be drift spraying, where the aircraft, flying amongst or just above the main body of locusts, sprayed at right-angles to the wind direction and used the flying locusts themselves for demarcation of spray runs. Large numbers of short spray runs were made in rapid succession over the densest portions of the swarm being treated until control was achieved. It was found that the spacing of the runs was not particularly important as long as each was applied in this way. The highly manoeuvrable Tiger Moths with a relatively slow operating speed were well-suited to this work although the small tank capacity of 50 gallons was a disadvantage.

A more even break-up of the spray into smaller droplets than that obtained with the equipment used is indicated. A high percentage of the kill has been shown to be due to droplets smaller than 100 μ (Rainey & Sayer, 1953) and these probably occupied a relatively small proportion of the total volume of the spray put out by the Tiger Moths. It was observed during early trials that the larger droplets fell almost directly below the aircraft while finer droplets drifted for 80–100 yards downwind under normal operating conditions. A spray sheet consisting almost entirely of even-sized, small droplets would be far more efficient in that a greater volume of effective insecticide could be distributed through the main concentrations of flying locusts on each run. A large number of short runs applied in rapid succession gave better results than long, single runs applied at intervals. It was possible that a cumulative effect of successive small and probably sub-lethal doses was responsible for a large percentage of the kill obtained, an effect that was indicated in the laboratory by MacCuaig (1957).

Once a successful method of treatment had been established, the success of the campaign as a whole rested largely on the strategic placing of the aircraft in the line of flight of oncoming swarms, an intimate knowledge of the terrain and

its effect on swarm movements, and the possession of an efficient information service for location of swarms. In the latter service, the aircraft were most useful for scouting and keeping track of travelling swarms. At Jerilderie, very large swarms were treated in a short time and many more locusts were killed than in the Hillston district, but the infestation was by no means controlled, as it had been at Hillston. This was due to the inability of the spraying party to plan a strategic campaign because of late arrival in the area. Swarms were already penetrating the more closely settled areas where they tended to disperse into smaller groups on patches of green feed. Suitable landing strips for the aircraft were difficult to locate here, particularly near irrigation settlements, and it was essential for the aircraft to work in close proximity to the swarm being treated because of the small tank capacity of each plane. It was concluded that control by aircraft (particularly light aircraft) had little application once swarms had entered such areas. Treatment of coherent, mobile swarms was satisfactory but spraying of loose or dispersed swarms was difficult and uneconomical.

It is considered that several units, each consisting of one or two light aircraft, placed strategically throughout the infestation area of the south-west of New South Wales in the spring of 1955, could have controlled the majority of the swarms surviving ground control measures against nymphal stages.

Spraying aircraft operating without the aid of ground markers have proved highly successful against mobile swarms of the Desert Locust, *Schistocerca gregaria*, in several large-scale operations (Rainey, 1957) and in one campaign the aircraft maintained continuous contact with incoming swarms for over 600 miles in Kenya and Tanganyika. The vulnerability of the rolling type of swarms to attack by light aircraft in the south-west of New South Wales and the importance of winds and topographical features in relation to swarm displacement would indicate a close similarity between *C. terminifera* and *S. gregaria* in these respects, and it is probable that the method of drift spraying by light aircraft could find a wide application against adult locust swarms in Australia, particularly as more information is accumulated on the relevant aspects of flight behaviour of swarms.

Summary.

A campaign in New South Wales against flying swarms of the Australian Plague Locust, *Chortoicetes terminifera* (Wlk.), using Tiger Moth light aircraft, is described. Large rolling swarms of this locust, travelling across the open plains of western New South Wales, are directed in their general south-easterly movement by natural barriers in such a way that regular migration routes are followed and predictions of swarm movements can be made. Of particular importance are the timber fringes of creeks and rivers which tend to baulk swarms temporarily and it was in such situations that locust swarms proved most susceptible to treatment by a manoeuvrable aircraft.

A technique of drift spraying was developed wherein aircraft were able to operate without ground direction against travelling swarms by spraying at right-angles to the wind direction and by using the main body of the flying locusts for demarcation. Large numbers of short spraying runs were made in rapid succession over the most dense portions of the swarm being treated until control was achieved. It was found that the spacing of the runs was not particularly important as long as each was applied to the densest portions of the swarm. The light and relatively slow-moving Tiger Moths proved highly suitable for this work and they were also useful for scouting and keeping track of swarms. Observations made after spraying indicated that the coherent flying swarms treated in the open plains were almost completely eliminated. If, however, swarms were able to reach closely settled or heavily timbered areas they tended to split and disperse and were difficult to treat. The insecticide used was an

emulsifiable concentrate containing 7 per cent. γ BHC, which was diluted with diesel oil, and one gallon of liquid containing 5·6 oz. of γ BHC was designed to cover one acre. However, as the campaign progressed, effective use of the spray was probably obtained at less than one gallon per acre, and a total area of 30–37 square miles of dense swarms was treated at a cost of approximately £13,700. There is scope for an improvement in the efficiency of the spraying technique as well as a reduction in some of the major costs in any future campaign.

It was considered that the campaign carried out in the Ivanhoe–Hillston district completely controlled all swarms in the area and protected from invasion valuable farming lands to the south-east. Further spraying operations, in the Jerilderie district, 150 miles away, were less successful, although many more locusts were killed. The spraying party arrived in the district too late to plan a strategic campaign and some swarms escaped treatment.

It is concluded that the method of aerial drift spraying is capable of wider application in Australia, particularly in areas where problems of distance, population and lack of facilities militate against successful control by ground machinery.

Acknowledgements.

This work was carried out by the New South Wales Department of Agriculture and the success of the campaign was largely due to the co-operative efforts of various Departmental and Pastures Protection Board Officers, particularly Mr. D. R. Stark, Field Officer of the Department of Agriculture, whose organising ability and intimate knowledge of the terrain were invaluable throughout the campaign, and Mr. E. L. Jones, Entomologist, whose thoroughness and accuracy in the appraisal of locust swarms for treatment enabled the unit to operate with maximum effectiveness. The considerable help received from these officers is gratefully acknowledged as is that from the senior pilot of the firm Aerial Agriculture, Mr. C. Coote, who was not only a capable pilot but also showed a keen and intelligent interest in the problem of locust spraying itself.

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Fig. 1. Typical appearance of country in the infestation area. Flat, open grassland with little timber except for the fringe along a creek in the distance.

Fig. 2. Tiger Moth aircraft spraying locusts massed along a line of timber near the Lachlan river in New South Wales.

REVISION OF THE GENUS *AMBLYPELTA* STÅL (HEMIPTERA, COREIDAE).

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(Plate XVIII.)

The genus *Amblypelta* was erected by Stål (1873) to include two species, *A. bilineata* Stål from New Caledonia (the genotype), and *A. nitida* Stål from Queensland. He distinguished it from *Dasynus* Burm. by the scutellum, which is equilateral (longer than broad in *Dasynus*) and truncate at the tip. Later, China (1934) described *A. cocophaga* from the Solomon Islands, and transferred *Pendulinus lutescens* Dist. to the genus *Amblypelta*. Further species were later added by Lever (1936) who described *A. gallegonis* from the Solomon Islands, and by Van Duzee (1940) who described *A. costalis* from Rennell I. Blöte (1935) described *A. fumosa* from New Britain, and *A. semifulva* from Timor and Wetter; the former, however, does not belong in this genus for reasons given later, while *A. semifulva*, described from female specimens only, should be regarded for the time being as a synonym of *A. lutescens* (Dist.). *Dasynus manihotis* Blöte, described by Blöte in the same work, is here transferred to the genus *Amblypelta* for reasons given later. Chadwick (1949) made *A. lutescens* (Dist.) a synonym of *A. nitida* Stål, but this is incorrect, examination of the holotypes showing them to be clearly distinct. The unique female type of *Cristovallia typica*, described by Distant (1920) from New Caledonia, has been examined and is clearly identical with *A. bilineata*. Evans (1952) included *Dasynus fuscescens* (Dist.) in *Amblypelta*, but this is incorrect; it should be retained in *Dasynus*. The species hitherto described which should be correctly placed in *Amblypelta* are therefore as follows:—

A. bilineata Stål 1873 (=*Cristovallia typica* Distant 1920). New Caledonia.
A. nitida Stål 1873. Queensland, N.S.W.
A. lutescens (Distant 1911) (includes *A. semifulva* Blöte 1935). Queensland, Timor, Wetter.
A. manihotis (Blöte 1935). Java.
A. cocophaga China 1934. Solomon Islands.
A. gallegonis Lever 1936. Solomon Islands.
A. costalis Van Duzee 1940. Bellona I.

During the course of investigations on immature nutfall of coconuts in the British Solomon Islands from 1954 to 1956, extensive collections were made of species of this genus, not only in these islands, but also in New Guinea, New Britain and Bougainville. In addition, material has been obtained for me by others in Australia, New Caledonia, New Guinea, New Ireland and Bougainville, and from various museums as acknowledged later. As a result, it has been possible to draw up a revision of the genus, involving redescriptions of certain species previously described, and the erection of five new species and five subspecies; this brings the total content of the genus to twelve species and five subspecies.

Genus **Amblypelta** Stål 1873.

The characters which separate this from other related genera of the tribe Dasynini have been reviewed by China (1934) and Brown (1955). The latter pointed out that the type material of *A. bilineata* (the genotype) differed considerably in the genitalia from other species added to the genus later; this has been confirmed with the help of additional material of this species obtained from New Caledonia (the original male type was badly damaged). On the other hand, the genitalia of *A. nitida*, which have now been studied, are also very different from those of *A. bilineata*, although on other characters these two species are obviously congeneric; it appears, therefore, that undue weight should not be given to the genitalia, and this genus should not be split on this character. There are certain other characters which vary considerably in the genus as it now stands; for instance, the existence of a pronotal collar, which is more or less pronounced in *A. gallegonis*, *A. cocophaga*, and certain other species here described for the first time, but is quite absent in *A. bilineata*, *A. nitida*, *A. lutescens* and *A. manihotis*. China (1934) has used this character in separating genera, but *A. lutescens* and *A. manihotis*, although resembling *A. bilineata* and *A. nitida* in lacking a pronotal collar, are obviously related in other ways to those species which have a collar (*e.g.*, in the form of the male parameres). There are certain other characters also which cut across each other if any attempt is made to split the genus; on one character it would have to be split at one level, and on other characters at other levels. Although the genus as it stands is unsatisfactory, it would be unwise to split it without at the same time making a thorough revision of the large genus *Dasynus* and other related Dasynine genera. This is impossible at the present time, but meanwhile the economic importance of species of *Amblypelta* has made a revision of the genus necessary. It appears best, therefore, to retain Stål's original character of the truncate tip to the scutellum as the diagnostic feature of the genus; the scutellum is not always equilateral in the genus as so defined, being sometimes longer than broad and sometimes broader than long. *Amblypelta fumosa* Blöte must be removed from the genus because the scutellum is not truncate; it was described from a single female from New Britain, but both sexes of a closely related species from the Solomon Islands have now been discovered, and it is found to differ from other larger species of *Amblypelta* in other characters also, such as the form of the male parameres (fig. 16 R). It seems best provisionally to place *fumosa* and this new species (described at the end of this paper) in the genus *Dasynus* Burmeister.

Key to the species of **Amblypelta.**

1. Antennae with segment I longer than IV, and III equal to IV; rostrum with basal segment longest; pronotum testaceous, concolorous except for slight infuscation of the anterior angles (fig. 1 A); abdominal segments I–V with a red spot on each side. (Pronotal collar absent; posterior margin of ♂ pygophore with a pair of prominent conical processes (fig. 1 B, C, E); ♂ paramere as in fig. 16 C) (Australia) .... *brevicornis*, **sp.n.**
   Antennae with segment IV usually longer than I, and always longer than III; rostrum with segment IV longer than or at least equal to I; pronotum with posterior part more or less infuscate (except in *manihotis*); abdomen without red lateral spots 2
2. Pronotum without trace of anterior collar (fig. 2 A, etc.); ♀ with transverse fissure of 7th ventral segment more or less sinuate (figs. 2 F, 3 G, 4 E); posterior dark area of pronotum narrow, with its anterior margin not or scarcely convex 3

Pronotum with anterior collar indicated and often pronounced; ♀ with transverse fissure of 7th ventral segment angulate, not or scarcely sinuate; posterior dark area of pronotum broader in the middle, with a strongly convex anterior margin (fig. 6 A) 7

3. Size usually larger (♂ 12·0–13·0 mm., ♀ 13·0–14·0 mm.); scutellum roundly truncate (fig. 4 D); surface usually dull between punctures; ♂ pygophore with a "shelf" across cavity (as in fig. 10 I); ♂ paramere rounded and reflexed apically, with a tooth half way along distal arm (fig. 16 D–F) 5

Size usually smaller (♂ 12 mm., ♀ 12·0–13·0 mm.); scutellum squarely truncate (figs. 2 D, 3 F); surface shining between punctures; ♂ pygophore without "shelf" across cavity (figs. 2 E, 3 E); ♂ paramere pointed apically, or with a small tooth at the tip (fig. 16 A, B) 4

4. Posterior infuscate area of pronotum darker; ♂ pygophore as in fig. 2 B, C; parameres very large and evenly tapered (fig. 16 A), protruding from a pair of grooves in its posterior margin (fig. 2 B, C); ♀ with two halves of IXth segment contiguous ventrally (fig. 2 F) (New Caledonia, New Hebrides) ...... *bilineata* Stål

Posterior infuscate area of pronotum paler; ♂ pygophore as in fig. 3 C, D; parameres smaller, constricted in the middle (fig. 16 B), invisible externally; ♀ with two halves of IXth segment not contiguous ventrally (fig. 3 G) (Australia) .... *nitida* Stål

5. Colour uniformly pale with contrasting dark punctures; pronotum relatively broader, without a dark posterior band, humeral angles slightly infuscate and turned upwards (fig. 5 A); surface very dull between punctures; (posterior margin of ♂ pygophore sinuate in ventral view, with two rounded lobes on either side of the middle line (fig. 5 C)) (Java) .... *A. manihotis* (Blöte)

Colour, except in very pale specimens, with contrasting dark and pale areas, the punctures concolorous; pronotum relatively narrower, with usually a dark band along the posterior margin and the humeral angles horizontal (fig. 4 A, H); surface less dull, sometimes slightly shining between punctures 6

6. ♂ pygophore relatively larger, the lateral processes more produced posteriorly and prominent in ventral view (fig. 4 C); colour usually paler, light and dark contrasts less pronounced; antennae shorter than head and body in both sexes (Australia and some islands to north) .... *A. lutescens lutescens* (Dist.) (incl. *semifulva* Blöte)

♂ pygophore relatively smaller, the posterior border more sinuate and the lateral lobes less prominent in ventral view (fig. 4 G); colour always darker, with strongly contrasting light and dark areas; antennae longer than head and body in males, equal to head and body in females (New Guinea) .... *A. lutescens papuensis*, **subsp.n.**

7. Colour sulphur- to orange-yellow, with extensive metallic black markings including the entire scutellum and elytra (except sometimes the costa), the posterior $\frac{4}{5}$ of the pronotum, and markings on the sides of the thorax; ♂ paramere characteristic (fig. 16 Q) 8

Colour otherwise, some shade of brown or chestnut above, with underside and anterior part of pronotum green or yellowish; scutellum with at most the tip blackened 9

8. Thorax with three discrete vertical black stripes on each side, at the posterior margins of the segments (fig. 15 B) (Bougainville, Choiseul) ...... *gallegonis bougainvillensis*, **subsp.n.**

Thorax with black lateral stripes more extensive and confluent in the dorsal part (fig. 15 A) (Ysabel) .... *gallegonis gallegonis* Lever

9. Hind femora with black tips; scutellum with truncate tip concolorous, sometimes slightly emarginate (figs. 6 D, 7 D) 10
Tips of hind femora not black; tip of scutellum infuscate, or if concolorous then squarely truncate and not emarginate 11
10. Pronotum with humeral angles strongly produced, acuminate (fig. 6 A); rostrum longer, reaching at least the posterior margin of the 3rd abdominal (2nd ventral) segment; ♂ pygophore as in fig. 6 B, C (New Guinea) .... *ardleyi*, **sp.n.**
Pronotum with humeral angles less produced (fig. 7 A); rostrum shorter, not or scarcely extending beyond the posterior coxae; ♂ pygophore as in fig. 7 B, C (New Guinea) .... *blötei*, **sp.n.**
11. Pronotum, viewed laterally, steeply declivous (fig. 8 F), and pronotal collar very pronounced (fig. 8 A); scutellum as long as or slightly longer than broad, the tip usually concolorous (fig. 8 D) (♂ pygophore as in fig. 8 B, C; rostrum long, reaching beyond the posterior margin of the 2nd abdominal (1st ventral) segment; antennae long and unusually slender (fig. 17 B)) (New Guinea) .... *theobromae*, **sp.n.**
Pronotum less declivous (fig. 8 G) and pronotal collar weaker; scutellum broader than long, with the tip infuscate (although sometimes very narrowly) 12
12. Relatively shorter and broader (Pl. XVIII, fig. 1); scutellum short, very strongly truncate and narrowly infuscate at tip (fig. 9 D); margin of costa without black stripe (♂ pygophore as in fig. 9 B, C) (San Cristobal) .... *cristobalensis*, **sp.n.**
Relatively longer and narrower (Pl. XVIII, fig. 2); scutellum much less strongly truncate; elytra with more or less well-marked black sub-costal stripe 13
13. Posterior margin of ♂ pygophore, viewed from behind, sinuate, the median part of it convex (fig. 10 J); parameres not or scarcely twisted (fig. 16 G, H); black sub-costal stripe very distinct and clearly defined 14
Posterior margin of ♂ pygophore, viewed from behind, concave in the median part (figs. 12 B, 13 B); parameres strongly twisted (fig. 16 M–P); sub-costal stripe weaker and poorly defined 15
14. ♂ pygophore smaller, not or scarcely exceeding 9th tergum, more strongly tapered and narrower posteriorly (figs. 10 B, C, 11 A–J); parameres with outer side of distal arm straight or scarcely concave (figs. 11 M–T, 16 G); pronotum with humeral angles less strongly produced (fig. 10 A, H, K); elytra paler, chestnut brown; 4th antennal segment with approximately the distal half black (fig. 17 F) (Guadalcanal, Nggela, Western Solomon Islands) *cocophaga cocophaga* China
♂ pygophore larger, extending beyond the 9th tergum, less tapered and more parallel-sided posteriorly (figs. 10 D, 11 K, L); parameres with outer side of distal arm strongly concave (figs. 11 U, V, 16 H); pronotum with humeral angles more produced and acuminate (fig. 10 F); elytra darker, chocolate brown; 4th antennal segment more narrowly and indistinctly black at the tip (fig. 17 E) (Malaita) .... *cocophaga malaitensis*, **subsp.n.**
15. Size smaller (♂ 11·5–12·7 mm., ♀ 13·0–13·8 mm.); rostrum relatively longer, reaching the posterior margin of the 2nd abdominal (1st ventral) segment; antennae with segment IV longer than I in ♂, equal to it in ♀ (fig. 17 H); colour of underside, when fresh, distinctly greenish (Rennell I.) *costalis rennellensis*, **subsp.n.**
Size larger (♂ 13·0–14·1 mm., ♀ 14·3–15·8 mm.); rostrum relatively shorter, reaching the middle of the 2nd abdominal segment; antennae with segment IV equal to I in ♂, shorter than I in ♀ (fig. 17 G–I); colour of underside, when fresh, usually yellowish rather than green 16

16. ♂ pygophore, viewed from behind, usually without a small notch in each side of the posterior border (fig. 12 B); lateral angles of pygophore, viewed from beneath, usually more rounded and lateral margins less convergent (fig. 12 C); parameres as in fig. 16 M, N (Bellona I.) .... *costalis costalis* Van Duzee

♂ pygophore, viewed from behind, usually with a small notch or groove in each side of the posterior border (fig. 13 B); lateral angles usually more pointed and lateral margins more convergent (fig. 13 C); parameres as in fig. 16 O, P (New Guinea, New Britain) ...... *costalis szentivanyi*, **subsp.n.**

Descriptions and Records of Species.

In addition to descriptions of new species and subspecies, those previously described are here partially redescribed where necessary, or additional details and figures are given to bring them into line with the system of description used in this work.

The material studied has been collected by the author, except where otherwise stated; additional material has been studied in the British Museum (Natural History), and loaned from other collections listed below. Types of new species and subspecies have been deposited in the British Museum (Natural History) unless otherwise stated. Additional named specimens of all species and subspecies have been deposited in the British Museum, and returned to or deposited in other collections; to indicate which species have been deposited in which collections the following abbreviations are used:

- (A) Australian Museum, Sydney.
- (B) Bernice P. Bishop Museum, Honolulu.
- (C) C.S.I.R.O., Canberra.
- (H) Hungarian National Museum, Budapest.
- (L) Rijksmuseum van Natuurlijke Historie, Leiden.
- (N) New South Wales Department of Agriculture, Sydney.
- (PM) Department of Agriculture and Stock, Port Moresby.
- (S) Naturhistoriska Riksmuseum, Stockholm.
- (SA) South Australian Museum, Adelaide.
- (SI) Department of Agriculture, Honiara, British Solomon Islands Protectorate.

Amblypelta brevicornis, sp.n.

Colour and punctuation. General body colour pale testaceous. Hemelytra with reddish suffusion (especially on the veins), the membrane slightly darker; without a dark costal stripe. Pronotum with the anterior angles and adjacent part of the lateral carinae sometimes slightly infuscate. Scutellum with the apex dark, blackish. Head testaceous, ocelli red. Underside pale testaceous, with a red spot on each side of abdominal segments I–V or II–V. Antennae with the entire basal segment, base and apex of segment II, apex of III and the distal two-thirds of segment IV (except the extreme tip) reddish (fig. 17 O); tarsi and apex of tibiae of the same colour. General surface dull between the punctures.

Head shorter than pronotum as 24:33. Ocelli slightly nearer the eyes than to the middle line of the head. Bucculae deepest anteriorly, the anterior angle slightly greater than 90°. Tylus porrect, projecting well forward. *Pronotum* broader than long as 49:33, the sides straight or slightly concave, the humeral angles acute but not prominent (fig. 1 A). No trace of an anterior collar. Scent gland with the posterior lobe of the peritreme about half as long as the aperture. *Scutellum* broader than long as 23:19, roundly truncate posteriorly, transversely

rugose (fig. 1 D). *Hemelytra* with cell *m-cu* rhomboidal, scarcely divergent posteriorly. *Antennae* short, just over $\frac{3}{4}$ as long as head and body combined, the segments relatively stout. Ratio of segments I–IV as 31:43:23:24 (♂ holotype). The terminal is much shorter than the basal segment, by comparison with any other species of the genus (fig. 17 O). *Rostrum* reaching the hind margin of the posterior acetabula, the ratio of segments I–IV as 22:18:12:17 (♂ holotype).

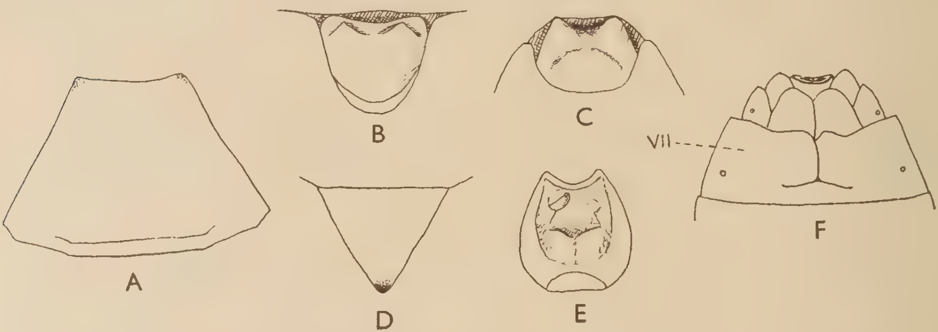

Fig. 1.—*Amblypelta brevicornis*, sp.n.: (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum; (E) ♂ pygophore from above, with left paramere and rectum removed; (F) tip of ♀ abdomen, ventral view. (A–E are drawn from the holotype.)

Male: pygophore characteristic (fig. 1 B, C), with a pair of strong conical protuberances at the posterior margin, and without a "shelf" across the inner cavity (fig. 1 E). Parameres slender, pointed, with a tooth on the inner side of the distal arm (fig. 16 C).

Female: transverse fissure of VIIth abdominal segment scarcely angulate in the middle, slightly sinuate (fig. 1 F).

Length 10·6 mm. (♂), 11·0–12·0 mm. (♀); width across humeral angles, 3·4 mm. (♂), 4·3 mm. (♀).

Distribution.

QUEENSLAND: 30 miles west of Collinsville, 12.vii.1950, 1 ♂ (holotype), 2 ♀♀ (*E. F. Riek*). NEW SOUTH WALES: Narrabri, 700 ft., 30.x.1924, 1 ♀ (*W. W. Froggatt*).

The holotype and 1♀ are deposited in C.

Amblypelta bilineata Stål (type species of *Amblypelta* Stål).

Amblypelta bilineata, Stål (1873, p. 74).

Cristovallia typica, Distant (1920, p. 581), **syn. nov.**

Stål's description of this species was short, and it is redescribed here from additional material obtained from New Caledonia.

Colour and puncturation. Hemelytra dark chestnut brown, the costal margins paler, the membrane transparent, showing the dark colour of the abdomen beneath; pronotum yellowish testaceous, the posterior border dark castaneous with black punctures; the anterior margin of this dark area is slightly concave and runs between the humeral angles (fig. 2 A). Scutellum paler than elytra, with the truncate apex black. Head usually testaceous with variably developed brown markings including a dark mark behind each ocellus and a pair of interrupted lines extending from the ocelli forwards to the antennal tubercles and beyond along the sides of the frontal processes. Underside entirely pale

testaceous. The upper surface, and most of the underside of the thorax is coarsely punctate, the surface strongly shining between the punctures. Antennae brownish-testaceous, with two well-marked blackish longitudinal lines on the basal segment, and most of segment IV and usually the tips of II and III dark brown (fig. 17 M). Legs pale testaceous to brownish, the tips of the tarsal segments darker brown.

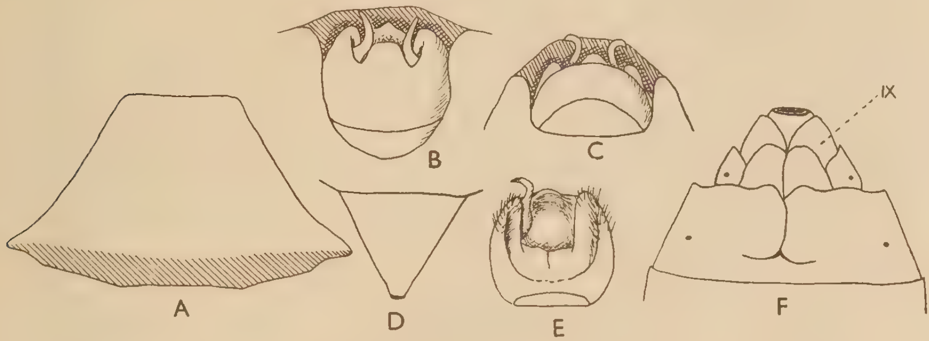

Fig. 2.—*Amblypelta bilineata* Stål: (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum; (E) ♂ pygophore from above, with left paramere and rectum removed; (F) tip of ♀ abdomen, ventral view.

Head shorter than pronotum as 25:37. Ocelli slightly nearer the eyes than to the median line of the head. Bucculae deepest at the anterior angle, which is obtusely rounded; tylus porrect. *Pronotum* broader than long as 62:37, the sides more or less concave, the humeral angles acute and somewhat prominent (fig. 2 A); no trace of an anterior collar. Scent gland with the posterior lobe of the peritreme very short, less than half as long as the aperture. *Scutellum* broader than long as 24:20, squarely truncate at the tip (fig. 2 D), punctate with a tendency towards transverse rugosity. *Hemelytra* with cell *m-cu* narrow at the base, divergent posteriorly, only slightly rhomboidal. *Antennae* from about $\frac{3}{4}$–$\frac{4}{5}$ as long as head and body combined, the ratio of segments I–IV as 31:45:28:38 (♂); the terminal segment is distinctly longer than either I or III (fig. 17 M). *Rostrum* reaching the middle of the posterior acetabula, the ratio of segments I–IV as 20:20:12:23 (♂).

Male: pygophore without a "shelf" across the inner cavity (fig. 2 E), with a pair of grooves in the posterior margin, from which the unusually long parameres protrude externally (fig. 2 B, C); parameres evenly tapered, with a small sub-apical tooth (fig. 16 A).

Female: transverse fissure of VIIth abdominal segment angulate in the middle, strongly sinuate; the two halves of the IXth segment contiguous ventrally in the middle line (fig. 2 F).

Length, 11·0–12·0 mm. (♂), 12·0–13·0 mm. (♀); width across humeral angles, 4·3 mm. (♂), 4·5–4·8 mm. (♀).

Distribution.

New Caledonia: Anse Vata, Noumea, 18–19.v.1956 on *Schinus terebinthifolius*, 15 ♂♂, 10 ♀♀, 8 larvae (*F. Cohic*); Noumea, 12.v.1956, on *Schinus terebinthifolius*, 3 ♀♀, several larvae (*C. P. Hoyt*). New Hebrides: Vila, Efate, vii.1925, 2 ♀♀ (*P. A. Buxton*).

Specimens are deposited in A, C, H, L, N, PM, S, SI.

The two specimens from the New Hebrides, amongst unworked material in the British Museum (Natural History), constitute an extension of the range of this species, hitherto only known from New Caledonia. They appear undoubtedly conspecific, but without males it is impossible to evaluate them on a subspecific basis.

Amblypelta nitida Stål.

Amblypelta nitida, Stål (1873, p. 75).

In the absence of sufficient material, a detailed redescription of this species will not be given, but in view of its recent confusion with *A. lutescens* (Dist.) (*e.g.*, Chadwick, 1949; Veitch & others, 1951), the main distinguishing features will be given. It resembles *A. bilineata* in general form and appearance.

Colour and puncturation. Very much paler than *A. bilineata*, pale testaceous throughout (at all events in dried specimens); the hemelytra, a narrow posterior border of the pronotum, two longitudinal stripes on antennal segment I and the distal half and base of segment II sometimes slightly darker (figs. 3 A, B, 17 N); tip of scutellum black. Puncturation a little closer than in *A. bilineata*, the surface between them shining.

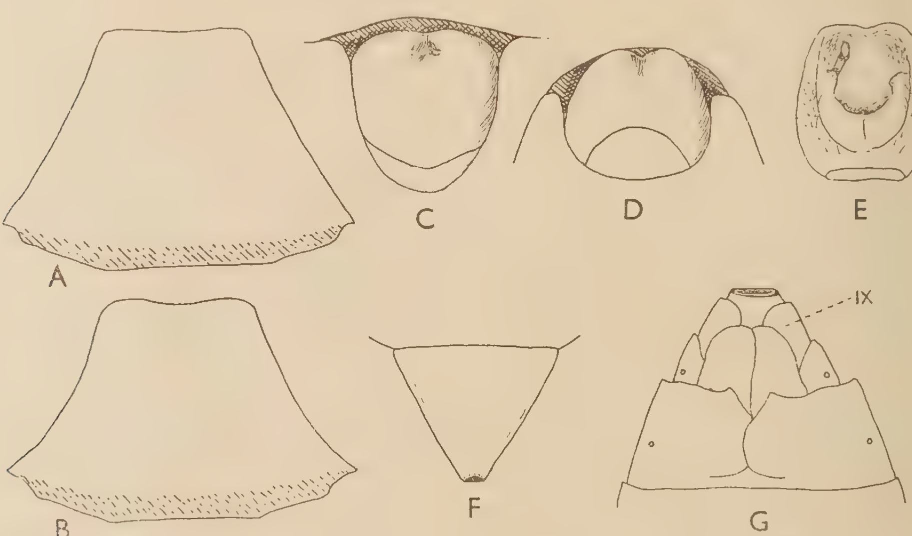

Fig. 3.—*Amblypelta nitida* Stål: (A, B) pronota of ♂ specimens from Queensland and N.S. Wales, respectively; (C) tip of ♂ abdomen in rear view; (D) the same in ventral view; (E) ♂ pygophore from above, with left paramere and rectum removed; (F) scutellum; (G) tip of ♀ abdomen in ventral view. (A, C, D and F are drawn from the holotype.)

Head shorter than pronotum as 26:39. *Pronotum* broader than long as 57:39, the sides almost straight (as in the holotype) to rather deeply concave (fig. 3 A, B); humeral angles usually less acute and prominent than in *A. bilineata*. *Scutellum* squarely truncate, broader than long as 22:20 (♂), with a tendency towards transverse rugosity (fig. 3 F). *Hemelytra* with cell *m-cu* much as in *A. bilineata*. Antennae about $\frac{4}{5}$ as long as head and body combined, the ratio of segments I–IV as 37:48:28:40 (holotype ♂). *Rostrum* usually reaching the middle of the 2nd abdominal segment, sometimes shorter, the ratio of segments I–IV as 22:19:14:26.

Male: pygophore very different from that of *A. bilineata* and other species, the posterior margin being entire except for a very slight median emargination, and the inner cavity without a "shelf" across the middle (fig. 3 C–E); parameres characteristic (fig. 16 B), not visible externally.

Female: abdomen much as in *A. bilineata* except that, in the few specimens examined, the two halves of segment IX are not contiguous ventrally (fig. 3 G).

Length, 12·0 mm. (♂), 12·5–14·0 mm. (♀); width across humeral angles, 3·8–3·95 mm. (♂), 4·1–4·7 mm. (♀).

Distribution.

New South Wales: Baulkham Hills, nr. Parramatta, 13.xi.1948, 2 ♂♂, 5 ♀♀, attacking peaches (*E. C. Levitt*); Narara, nr. Gosford (just north of Sydney), iv.1950, 1 ♀ (*A. Dyce*); Chatswood, nr. Sydney, x.1949, 1 ♀ (*A. Dyce*); 23.viii.1956, 1 ♀ (*C. E. Chadwick*); Mosman, 26.x.1948, causing "pitting" on peaches, 4 ♂♂, 2 ♀♀; Sydney, 26.xi.1901, 1 ♂ (*G. Froggatt*); xii.1955, 1 ♂; Warawee, 12.xii.1928, attacking fruit trees, 3 ♂♂, 1 ♀ (*J. B. Grant*). Queensland: Brisbane, 1 ♀ (*H. Hacker*).

Specimens are deposited in C, N, S.

The type locality is Rockhampton, and Blöte (1935) has reported it from Peak Downs; both these localities are in Queensland, but other records suggest that this species extends further south as a general rule, almost as far as Sydney, and is replaced by *A. lutescens* towards the north.

Amblypelta lutescens lutescens (Dist.).

Pendulinus lutescens, Distant (1911, p. 581).
Amblypelta lutescens, China (1934, p. 188).
Amblypelta semifulva, Blöte (1935, p. 215) **syn. nov.**
Amblypelta lutescens, Lepesme & others (1947, p. 94).
Amblypelta nitida, Chadwick (1949).
Amblypelta nitida, Veitch & others (1951, p. 264).

Distant's original description requires supplementing in certain details, with the help of more extensive material.

Colour and puncturation. General body colour pale testaceous in dried specimens, but stated to be pale green in life; hemelytra usually pale testaceous in Queensland forms, but sometimes chestnut-brown, in which case an indistinct darker sub-costal stripe may be present; membrane transparent, sometimes infuscate blackish. Pronotum anteriorly pale greenish testaceous, with a narrow band along posterior border darker (fig. 4 A, H); the anterior margin of this band is straight or very slightly convex, running between the humeral angles; this posterior band matches the colour of the elytra, being little darker than the anterior part of the pronotum in paler specimens, but in others deep chocolate brown. Scutellum coloured as the hemelytra, or somewhat paler, with the tip black. Head and underside coloured as the anterior part of the pronotum, unmarked. Antennae testaceous with a longitudinal black dorsal line on segment I, the tips of II and III and the distal half and base of IV infuscate, blackish, but these markings vary in intensity, with the general pigmentation of the insect (fig. 17 K). Legs brownish testaceous. Puncturation of general surface coarse, the surface dull or slightly shining between the punctures.

Head shorter than pronotum as 25 : 39; ocelli equidistant between eyes and median line of head; bucculae deepest near anterior end, the angles broadly rounded; tylus porrect. *Pronotum* broader than long as 56 : 39 (this figure varies); lateral margins almost straight or somewhat concave (fig. 4 A, H). Humeral angles acute but not strongly produced, although very variable in this respect; no trace of an anterior collar. Scent glands with posterior lobe of the peritreme

about half as long as the aperture. *Scutellum* with the width equal to or very slightly greater than the length, the tip roundly and not strongly truncate (fig. 4 D, I); coarsely punctate and transversely rugose. *Hemelytra* with cell *m-cu* somewhat rhomboidal, divergent or almost parallel-sided. *Antennae* shorter than head and body combined, by about 1 mm. in males and 2–3 mm. in females; ratio of segments I–IV as 40:45:30:37 (♂), but this is variable; segment IV is rarely longer than I and usually shorter (fig. 17 K). *Rostrum* short, reaching the anterior margin or middle of the posterior acetabula; ratio of segments I–IV as 20:19:13:23.

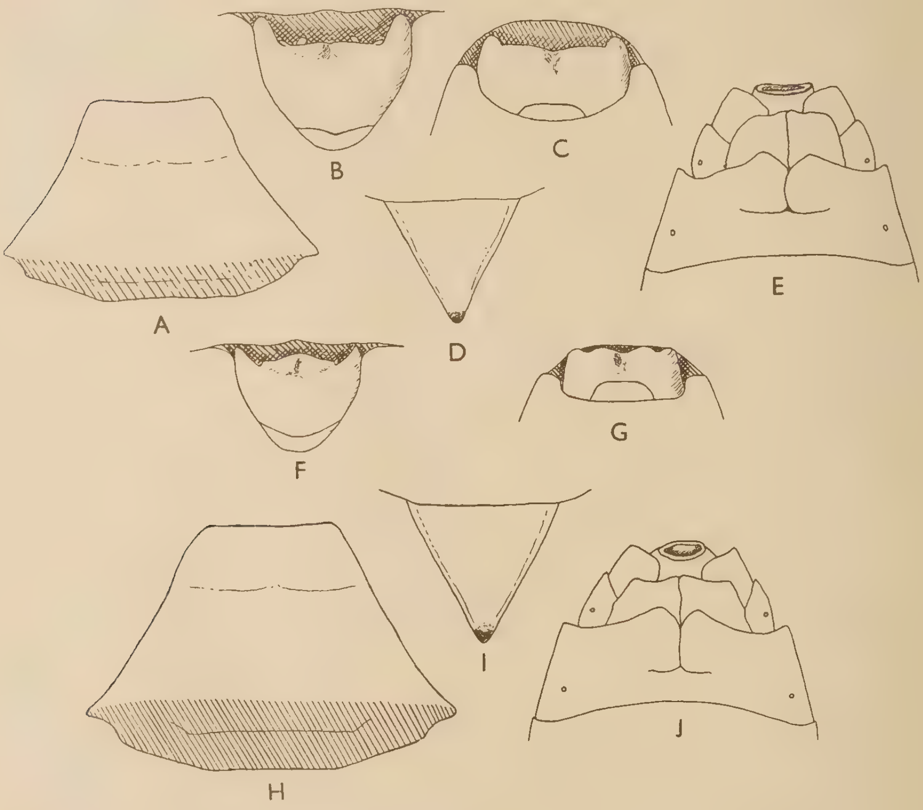

Fig. 4.—*Amblypelta lutescens lutescens* (Dist.): (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum (A–D are drawn from the ♂ holotype); (E) tip of ♀ abdomen, ventral view; (H) pronotum (♀, Kai Is.); (I) scutellum (♀, Timor); (J) tip of ♀ abdomen, ventral view (specimen from Wetter).
Amblypelta lutescens papuensis, subsp. n.: (F) tip of ♂ abdomen, rear view; (G) the same in ventral view.

Male: pygophore short and truncate as seen from below (fig. 4 C), with a broad, flat emargination in the posterior border as seen from behind (fig. 4 B); parameres rounded at the re-curved tip, with a small tooth half way along the distal arm (fig. 16 D).

Female: transverse fissure of VIIth abdominal segment scarcely angulate, almost straight, slightly sinuate (fig. 4 E, J).

Length, 11·6–13·1 mm. (♂), 12·4–15·0 mm. (♀); width across humeral angles, 3·5–4·2 mm. (♂), 4·2–4·75 mm. (♀).

Distribution.

QUEENSLAND: A few specimens have been examined: Cairns, 3.viii.1938, 2 ♂♂, 3 ♀♀; Redlynch, 16.viii.1938–14.xii.1938, 3 ♂♂, 7 ♀♀ (*Papuan Australian Expedition*); Byfield, 23.iii.1926, 1 ♂, on banana (*J. L. Froggatt*); 27.ii.1937, 1 ♂, 1 ♀ (*J. S. Phillips*); Thursday Is., 1 ♀ (*N. B. Tindale*). NORTHERN TERRITORY: Darwin, 1 ♂, without date (*G. F. Hill*). This is a very small specimen (11·0 mm.) but agrees in all essential details with Queensland specimens. MURRAY Is. (Gulf of Papua): 1 ♂, 1 ♀ (no other data); 1 ♀ (*A. M. Lea*). BANKS I. (Torres Strait): 1910, 1 ♂ (*Elgner*, *ex* coll. *W. W. Froggatt*). KAI Is.: 2 ♀♀, one from Toeal, otherwise without locality data (see below); 1 ♀, without further detail (*Wallace*).

Specimens have been deposited in C, H, L, N, PM, SA, SI.

With *A. semifulva* Blöte placed as a synonym of *A. lutescens lutescens* (see p. 509), Timor and Wetter should be added to the distribution which is now shown to be very wide, embracing most of northern Australia, and several of the islands to the north. The species is very variable, in size, colour and the shape of the pronotum. Queensland specimens tend to be pale, while island forms are much darker and the contrast between light and dark areas of the pronotum is more distinct. In this the island forms resemble the ssp. *papuensis*, but the specimens from Banks I. and Murray Is. clearly belong to the type form on the shape of the male pygophore. The Timor, Wetter and Kai Is. forms (*semifulva* Blöte) are unfortunately known only from females, but their general resemblance to the Banks I. and Murray Is. specimens makes it preferable to include them in the type form rather than in ssp. *papuensis*, at least until males can be studied; their darker colour, in any case, can be matched in certain Queensland specimens. With more material from these and other islands it may be necessary to erect further geographical subspecies.

The specimen from Toeal in the Kai Is. (in the Hungarian National Museum) bears a label "*Amblypelta obscura* Bredd. n.sp., holotypus". I cannot so far trace any publication of this name and so it should be disregarded. If it should subsequently turn out to have been published, however, the date of publication will decide whether it is a synonym of Distant's name, or whether it has priority; in the latter case it would be necessary to study much more material from the Kai Is. before deciding whether the two forms really are conspecific, before sinking a name as well-known as *A. lutescens*.

Amblypelta lutescens papuensis, subsp. n.

Specimens from the New Guinea mainland differ from Queensland material in the following characters:—

Colour: they are always darker, the contrast between chocolate-brown and pale areas being well marked. The type form from Queensland is usually paler, with the contrast less distinct; but the character is not a good one, since specimens from the smaller islands, and some of those from Queensland, are as dark as New Guinea specimens.

Antennae: in the type form from Queensland the antennae are always shorter than the head and body combined in both sexes, by about 1 mm. in males and 2–3 mm. in females; in Papuan specimens they are equal to the head and body in females, and longer by up to about 0·5 mm. in males (fig. 17 L).

Male pygophore: the pygophore is relatively larger and broader in the type form, and the lateral lobes project posteriorly so as to be clearly visible in ventral view (fig. 4 C); the posterior margin between them is broadly emarginate, flat in posterior view (fig. 4 B). In the Papuan form the pygophore is smaller,

especially the lateral lobes which are scarcely visible in ventral view, and the posterior margin between them is sinuate and convex in rear view (fig. 4 F). In this character ssp. *papuensis* is intermediate between the type form and *A. manihotis*.

Pronotum: the lateral margins tend to be more concave in Papuan specimens.

Length: Papuan specimens are shorter on the average (length of males about 12·0 mm. and of females 12·4–14 mm.).

These last two characters are not reliable, however, and specimens of the type form can be found to match Papuan specimens.

The paramere of ssp. *papuensis* is illustrated in fig. 16 E.

Distribution.

Papua, New Guinea: Mt. Lamington, 1,300–1,500 ft., 2 ♂♂, 1 ♀ (*C. T. McNamara*); Kuiaro, Samarai, 6.iii.1954, 2 ♀♀, on *Phaseolus* (*W. Cottrell-Dormer*); Bisianumu, nr. Port Moresby, 1,600 ft., 16.ix.1955, 1 ♂, 1 ♀, on *Hevea brasiliensis* (*J. J. H. Szent-Ivany*); 19.iii.1956, 12 ♂♂ (including holotype), 10 ♀♀, 1 larva, on *Hevea* and *Manihot*; Brown River, nr. Port Moresby, 21.v.1956, 1♂, 3 ♀♀ (*J. J. H. Szent-Ivany*).

Specimens have been deposited in A, C, L, PM, SA, SI.

A single female specimen in the collections of the British Museum (Natural History), from the Mimika River, New Guinea, is possibly referable to *A. l. lutescens*, but is larger (length 15·2 mm.) and has the 1st antennal segment considerably longer (the other segments are missing).

Another single female in the British Museum labelled "Lombok, 1,500 ft., June '96 (*Everett*)" also seems to be closely related to *A. l. lutescens*, but is distinct in certain characters. The antennal segments are longer; as compared with a female *A. l. lutescens* from Queensland of the same length (15 mm.) the measurements of the segments are as follows:—

	I	II	III	IV
A. l. lutescens	38	44	30	43
♀ from Lombok ...	60	60	36	(missing)

Also the pronotum has a very slight indication of an anterior collar, the transverse fissure of abdominal segment VII is scarcely sinuate, and the scutellum is not truncate, although it is darkened apically. On this last character it should not be placed in *Amblypelta* at all, and yet it is obviously related and in other features shows an intermediate condition between *A. l. lutescens* and other larger species. Until more material, and particularly males, can be studied, it is not possible to say more about this specimen.

The Mimika River specimen does not conform to ssp. *papuensis*, nor does the Lombok specimen approach *A. manihotis* in structure, in spite of its geographical proximity. It is probable that when more material is available from New Guinea and the islands, *A. lutescens* may prove to be a widespread polytypic species with several subspecies.

Amblypelta manihotis (Blöte).

Dasynus manihotis, Blöte (1935, p. 212), **syn. nov.**
Dasynus manihotis, Phillips (1941, figs. 7–8).

From the roundly truncate, infuscate tip of the scutellum and the form of the head, and from the very obvious relationship to *A. lutescens* in the form of the pronotum and in the male and female genitalia, and especially the male parameres, there is no doubt that this species should be included in *Amblypelta*. The following details are added to Blöte's description for conformity with other descriptions in this revision.

Colour and puncturation. Hemelytra fawn-testaceous, without dark subcostal stripe; a spot near the apex of the corium and another near its inner corner paler; membrane blackish. Pronotum of the same colour, unicolorous or slightly more darkly punctured posteriorly, the humeral points slightly infuscate. Scutellum as the posterior part of the pronotum, the tip deeply infuscate. Head and underside pale testaceous, ocelli pink. Antennae pale brownish testaceous, the distal $\frac{2}{3}$ and base of segment IV and sometimes apex of II and III blackish. Legs pale testaceous, tarsi slightly darker. Puncturation coarse and mostly deep, the punctures dark brown over most of the upper surface; surface between punctures dull.

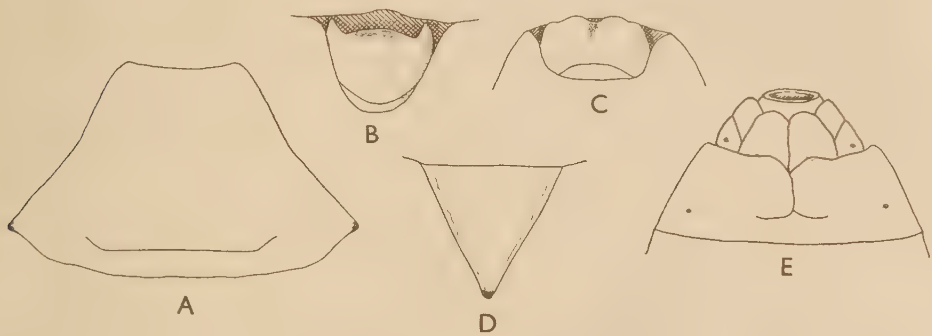

Fig. 5.—*Amblypelta manihotis* (Blöte): (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum; (E) tip of ♀ abdomen, ventral view.

Head shorter than pronotum as 25:40; ocelli slightly nearer to eyes than to median line of head (5:6); bucculae deepest at anterior angle, which is distinct, slightly obtuse; tylus moderately produced, moderately porrect. *Pronotum* broader than long as 65:40; side margins slightly concave, humeral angles acute and moderately produced, directed somewhat upwards; anterior collar absent (fig. 5 A). Scent gland with posterior lobe of peritreme $\frac{2}{3}$ as long as the aperture. *Scutellum* with median length equal to width, the apex moderately and roundly truncate (fig. 5 D) as in *A. lutescens*; coarsely punctate, not or scarcely transversely rugose. *Hemelytra* with cell *m-cu* almost rectangular, scarcely rhomboidal, usually slightly divergent posteriorly. *Antennae* about 1 mm. shorter than head and body combined in female (no male available with antennae complete); ratio of segments I–IV as 50:53:33:(missing) in male, and as 47:52:31:38 in female. *Rostrum* reaching the hind border of the posterior acetabula, the ratio of segments I–IV as 19:20:15:24 (♂).

Male: pygophore with the posterior margin sinuate viewed from below (fig. 5 C), a central emargination being bounded by a rounded lobe on each side; the lateral lobes, visible in posterior view (fig. 5 B) are scarcely visible from below. Parameres (fig. 16 F) almost as in *A. lutescens*.

Female: the transverse fissure of the VIIth abdominal sternum sinuate (fig. 5 E), as in *A. lutescens*.

Length, 12·5 mm. (♂), 12·5–14·0 mm. (♀) (these accord with Blöte's figures except that 1 ♀ in the British Museum is much smaller than in his range); width across humeral angles, 4·5 mm. (♂), 4·1–4·8 mm. (♀).

Distribution.

Java: 1 ♂ and 6 ♀♀ in the British Museum (Natural History), from Wonogiri (*J. S. Phillips*) and Kederi.

Amblypelta ardleyi, sp.n.

Colour and puncturation. Hemelytra warm chestnut brown, with an indistinct blackish subcostal stripe; membrane transparent, smoky. Pronotum ochreous yellow anteriorly (in dried specimens); a broad posterior band, convex on its anterior border, of the same colour as the elytra; humeral spines yellowish brown. Scutellum as the elytra, the tip not or scarcely infuscate. Head ochreous yellow, with a small brown spot on the posterior border of each ocellus. Underside ochreous yellow; antennae of the same colour, the tips of segments II and III, the distal $\frac{2}{3}$ and extreme base of IV black, and a thin longitudinal, distally dilated dorsal line on I, black (fig. 17 C). Legs ochreous yellow with a conspicuous black band at the tip of the hind femur. Puncturation coarse and deep on the pronotum; shining between the punctures on the anterior part of the pronotum, elytra dull.

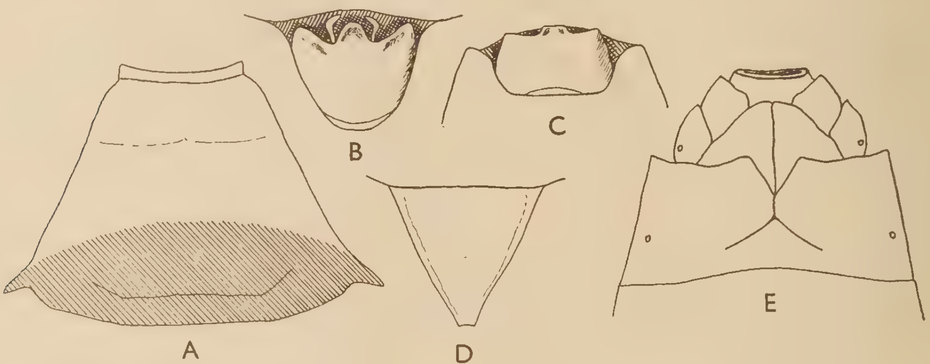

Fig. 6.—*Amblypelta ardleyi*, sp.n.: (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum; (E) tip of ♀ abdomen, ventral view.

Head shorter than pronotum as 37:45; ocelli very slightly nearer the eyes than to the median line of the head; bucculae deepest at the anterior angles, which are well marked, a little greater than right angles; tylus very long, porrect. *Pronotum* broader than long as 73:45; side margins straight except posteriorly; humeral angles very sharp and prominent, and directed somewhat upwards; anterior collar well developed (fig. 6 A); upper surface strongly declivous viewed from the side, as in *theobromae* (fig. 8 F), but less convex. Scent gland with the posterior lobe of the peritreme about $\frac{1}{2}$ as long as the aperture. *Scutellum* as long as broad; tip squarely truncate, sometimes emarginate in the middle (fig. 6 D); deeply punctate and not or scarcely transversely rugose. *Hemelytra* distinctly convergent posteriorly; cell *m-cu* rhomboidal, divergent posteriorly. *Antennae* and legs long; antennae 4–5 mm. longer than head and body in males, 3–4 mm. longer in females; ratio of segments I–IV as 68:93:57:71 (♂ holotype). *Rostrum* very long, nearly reaching the posterior margin of the 4th abdominal segment; ratio of segments I–IV as 38:40:28:58 (♂).

Male: posterior margin of pygophore with a rounded central lobe, concave on its outer surface, separating two lateral emarginations (fig. 6 B, C); central cavity with a transverse " shelf "; paramere with distal arm bent upwards at the tip (fig. 16 K).

Female: transverse fissure of the VIIth abdominal sternum sharply angled (fig. 6 E).

Length, 15·5–16·0 mm. (♂), 17·0 mm. (♀); width across humeral angles, 4·9–5·1 mm. (♂), 5·1–5·5 mm. (♀).

Distribution.

PAPUA, NEW GUINEA: Bubia, nr. Lae, 25–27.x.1956, in native gardens, 3 ♂♂, 2 ♀♀ (including ♂ holotype) (*J. H. Ardley*).

Specimens have been deposited in PM.

Amblypelta blötei, sp.n.

Colour and puncturation. Hemelytra dark brown, with a very indistinct darker subcostal stripe; membrane transparent, smoky. Pronotum testaceous anteriorly, with the posterior border broadly chocolate brown; the anterior margin of this brown band is sinuous (fig. 7 A); humeral angles almost black. Scutellum coloured as the elytra, the tip concolorous. Head brownish testaceous, with a dark brown mark behind each ocellus. Underside testaceous. Antennae brown, the tips of segments I–III, a thin dorsal longitudinal line on I, and the distal $\frac{3}{4}$ and base of IV black (fig. 17 D). Legs brownish testaceous, an apical band on the posterior femur black. Puncturation coarse, rather sparse over the anterior part of the pronotum, which is strongly shining between punctures.

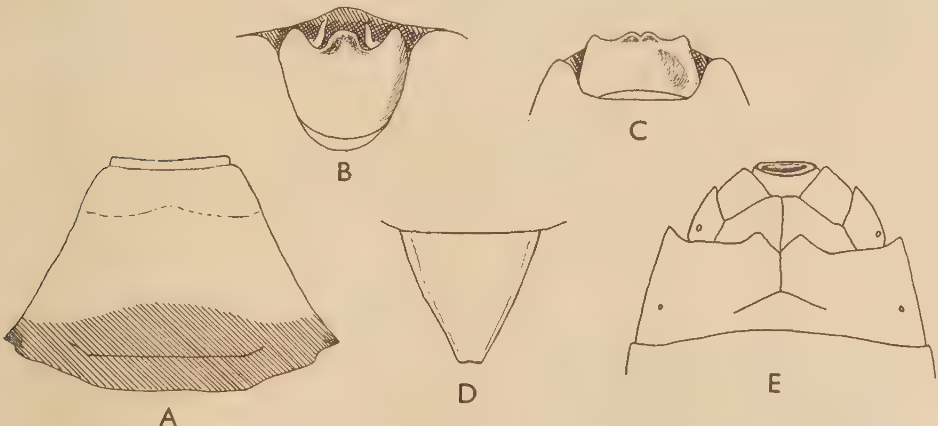

Fig. 7.—*Amblypelta blötei*, sp.n.: (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum; (E) tip of ♀ abdomen, ventral view.

Head shorter than pronotum as 26:39. Ocelli equidistant from the eyes and the median line of the head; bucculae deepest at the anterior angles, which are obtuse and slightly rounded. Tylus somewhat declivous in lateral view. *Pronotum* broader than long as 55:39; side margins almost straight; humeral angles acute but not prominent; anterior collar well marked, narrow (fig. 7 A); scent gland with posterior lobe of peritreme slightly more than half as long as the aperture (8:13). *Scutellum* as long as broad; truncate tip slightly emarginate centrally; coarsely but sparsely punctured, with scarcely any indication of transverse rugosity. *Hemelytra* not convergent posteriorly as in *ardleyi*; cell *m-cu* rhomboidal, divergent posteriorly. *Antennae* about 2·5 mm. longer than head and body combined in male; ratio of segments I–IV as 62:68:44:?59 (damaged) (♂). *Rostrum* short, not extending beyond hind margin of posterior acetabula; ratio of segments I–IV as 24:22:16:27 (♂).

Male: central lobe in posterior margin of pygophore indented in the middle (fig. 7 B–C); paramere with distal arm less bent upwards apically than in *ardleyi* (fig. 16 L).

Female: transverse fissure in VIIth abdominal sternum distinctly angulate (fig. 7 E).

Length, 13·5 mm. (♂), 14 mm. (♀); width across humeral angles, 3·8 (♂), 4·1 mm. (♀).

Distribution.

Dutch New Guinea: "Araucaria Camp", in valley of Araucaria River (tributary of Sahuweri River), 800 m., 11.iii.1939, 2 ♂♂ including holotype (*L. J. Toxopeus*); "Rattan Camp", on ridge sloping into Araucaria River, 1,200 m., 13.ii.1939, 1 ♀ (*L. J. Toxopeus*).

The holotype and ♀ are deposited in L, the remaining specimen in the British Museum (Natural History).

Amblypelta theobromae, sp.n.

Colour and puncturation. Hemelytra dull brown, a narrow subcostal stripe slightly but indistinctly darker than the remainder; membrane transparent, slightly blackish. Pronotum greenish testaceous, with a broad band along the posterior margin brown, this band including the humeral angles and having a convex anterior border (fig. 8 A). Scutellum coloured as elytra, the tip usually concolorous, sometimes indistinctly infuscate. Head testaceous, with a narrow reddish brown ring round each ocellus. Underside and legs yellowish testaceous.

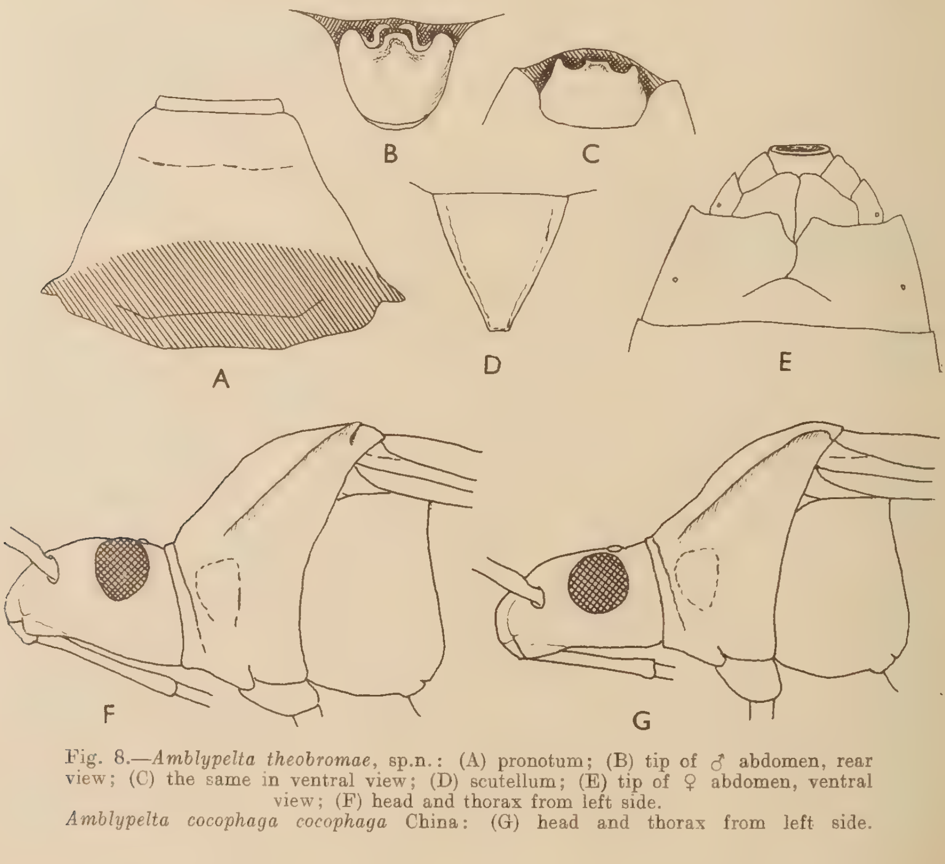

Fig. 8.—*Amblypelta theobromae*, sp.n.: (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum; (E) tip of ♀ abdomen, ventral view; (F) head and thorax from left side.
Amblypelta cocophaga cocophaga China: (G) head and thorax from left side.

Puncturation rather coarse, distantly spaced on the anterior half of the pronotum, which is strongly shining between the punctures; posterior part of pronotum, scutellum and hemelytra dull between the punctures. Antennae of the same colour, with distinct black markings as follows: a dorsal longitudinal streak on segment I, the apices of segments I–III, the distal half and extreme base of segment IV.

Head shorter than pronotum as 28:42. Ocelli equidistant from the eyes and the median line of the head. Bucculae deepest at the anterior angle, which is well-marked and slightly obtuse. Tylus slightly more declivous than in other species, less porrect. *Pronotum* broader than long as 60:42, strongly declivous anteriorly (fig. 8 F). Lateral margins almost straight, the carinae weak. Humeral angles acute and prominent; anterior collar well developed (fig. 8 A). Scent gland with posterior lobe of peritreme over half as long as the aperture. *Scutellum* as long as, or slightly longer than broad, the apex squarely truncate, the sides distinctly margined (fig. 8 D). *Hemelytra* with cell *m-cu* rhomboidal, the sides either parallel or divergent posteriorly. *Antennae* very long (about $\frac{1}{4}$–$\frac{1}{3}$ as long again as head and body combined) and very slender (fig. 17 B). Ratio of segments I–IV as 71:83:53:64 (♂ from Lae); in specimens from Popondetta the terminal segment is relatively longer (ratio 72:80:52:70). *Rostrum* reaching a little beyond the hind margin of the 2nd abdominal (1st ventral) segment, the ratio of segments I–IV as 31:29:23:38 (♂).

Male: pygophore with a pair of deep grooves in the posterior margin, separated by a tongue which is concave on its external surface (fig. 8 B, C); paramere as in fig. 16 I.

Female: transverse fissure in VIIth abdominal segment angulate, not sinuate (fig. 8 E).

Length, 14·0–15·0 mm. (♂), 15·5–17·8 mm. (♀); width across humeral angles, 4·1–4·5 mm. (♂), 4·7–5·6 mm. (♀).

Distribution.

PAPUA, NEW GUINEA: Simbang, Huon Gulf, 8.xii.1898, 1 ♀ (*Biro*); Mt. Lamington, vi.1927, 1 ♂; i–ii.1929, 1 ♀ (*C. T. McNamara*); Mt. Lamington, 1,300–1,500 ft., 1 ♂, 1 ♀ (*C. T. McNamara*); Wum, Upper Jimmi Valley, 17.vii.1955, 1 ♀ (*J. L. Gressitt*); Sangara, Popondetta, 8/9.xii.1955, 3 ♂♂, 2 ♀♀, 3 larvae (*J. J. H. Szent-Ivany*); 20.iii.1956, 4 ♂♂, 3 ♀♀, 2 larvae; 21.iii.1956, 7 ♂♂, 10 ♀♀ (including 2 pairs mating), larvae; 22.iii.1956, 4 ♂♂, 4 ♀♀, 1 larva; 23.iii.1956, 4 ♂♂, 3 ♀♀ (including 1 pair mating), larvae; Kunkamen, near Lae, 21.xi.1956, 2 ♂♂, 5 ♀♀ (including 1 pair mating), 3 larvae; Leiwomba, near Lae, 22.xi.1956, 1 ♂, 1 ♀, 4 larvae; Wareo, Finschhafen, 1 ♂ (Rev. *L. Wagner*).

Specimens are deposited in A, B, C, H, L, PM, SA, SI

All those taken at Lae in 1956, and most of those taken in the Popondetta district, were collected on the fruits of cacao (*Theobroma cacao*), of which crop this species is a potentially serious pest; a few were collected on rubber (*Hevea brasiliensis*), and one on cassava (*Manihot esculenta*). The species seems to be widely distributed in eastern New Guinea, possibly up to a high altitude (*e.g.*, Upper Jimmi Valley).

Amblypelta cristobalensis, sp.n.

Colour and puncturation. Hemelytra dark chocolate brown, without trace of a black subcostal stripe; membrane transparent, slightly smoky. Pronotum pale greenish testaceous, with a posterior brown band of moderate width, its anterior border slightly convex (fig. 9 A); humeral angles brown. Scutellum coloured as elytra, the truncate apex narrowly black. Head brownish green, with blackish markings behind the ocelli and on the antennal tubercles. Underside pale

greenish testaceous. Antennae brown, the tips of segments I–III, a dorsal longitudinal line on I. the distal half and base of IV black. Legs greenish testaceous, the distal part of the femora with the tibiae and tarsi, slightly brownish. Punctuation coarse, the surface shining on the anterior part and underside of the thorax.

Head shorter than pronotum as 27:40. Ocelli very slightly nearer the eyes than to the median line of the head. Bucculae deepest at anterior angle, which is very obtuse and rounded. Tylus porrect, moderately produced. *Pronotum*

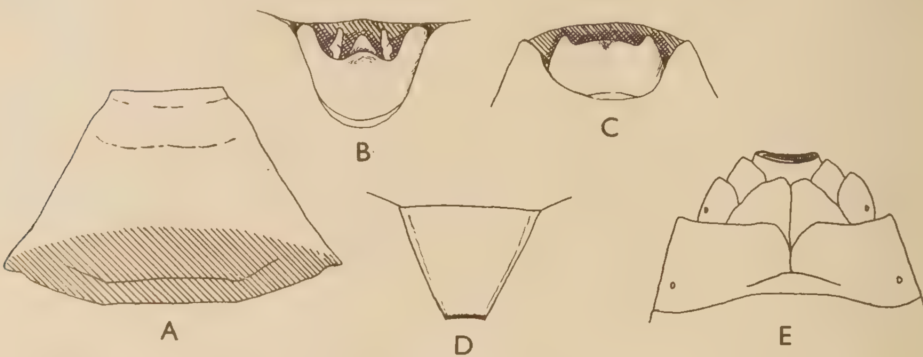

Fig. 9.—*Amblypelta cristobalensis*, sp.n.: (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum; (E) tip of ♀ abdomen, ventral view.

broader than long as 66:27; side margins straight or slightly concave; humeral angles acute, moderately produced; anterior collar feebly indicated (fig. 9 A). Scent gland with posterior lobe of peritreme about half as long as the aperture. *Scutellum* very short and strongly truncate (fig. 9 D), broader than long as 25:21 in males, 30:23 in females; coarsely and irregularly punctate and somewhat transversely rugose. *Hemelytra* slightly convergent posteriorly, cell *m-cu* very slightly rhomboidal and parallel-sided. *Antennae* slightly longer than head and body combined in males, slightly shorter in females; ratio of segments I–IV as 49:60:39:48 (♂ holotype). *Rostrum* reaching approximately the posterior margin of the 2nd abdominal segment; ratio of segments I–IV as 26:24:17:30.

Male: pygophore with posterior margin sinuate (fig. 9 B, C); paramere with apex of distal arm strongly attenuated, not reflexed (fig. 16 J).

Female: transverse fissure of VIIth abdominal sternum rather bluntly angled in the middle (fig. 9 E).

Length, 12·0–12·5 mm. (♂), 13·0–13·75 mm. (♀); width across humeral angles, 4·1 mm. (♂), 4·5–4·8 mm. (♀).

Distribution.

San Cristobal, Solomon Islands: Maru Bay, 2.v.1955, in coconut plantation, 1 ♀ (emerged late from nymph); Boroni, 14.vi.1955, 11 ♂♂ (including ♂ holotype), 5 ♀♀, 1 larva on *Manihot*; 14.x.1955, 14 ♂♂, 9 ♀♀, 13 larvae, on *Manihot*.

Specimens are deposited in B, C, H, L, PM, SA, SI.

This species, easily distinguished from *A. cocophaga* by its short, stumpy appearance and strongly truncate scutellum (Pl. XVIII, fig. 1), appears to be endemic on San Cristobal I.

Amblypelta cocophaga cocophaga China.

Amblypelta cocophaga, China (1934, p. 187).

There is little to add to China's description of this species, recognised as an important coconut pest by Lever, who had earlier described it as an unnamed species of *Dasynus* (Lever, 1933). It has also been described by Phillips (1940). With its parallel form and clearly defined, black subcostal stripe and characteristic male pygophore it is distinct from any other species (Pl. XVIII, fig. 2).

Structural details are given in fig. 8 G, figs. 10 and 11, and the antenna is illustrated in fig. 17 F. The male paramere (fig. 16 G) has not been figured before.

It has become necessary as the result of studying a large amount of material to erect a subspecies for the Malaita form, which is described later. There is some variation over the remainder of its range, especially the Western Solomon

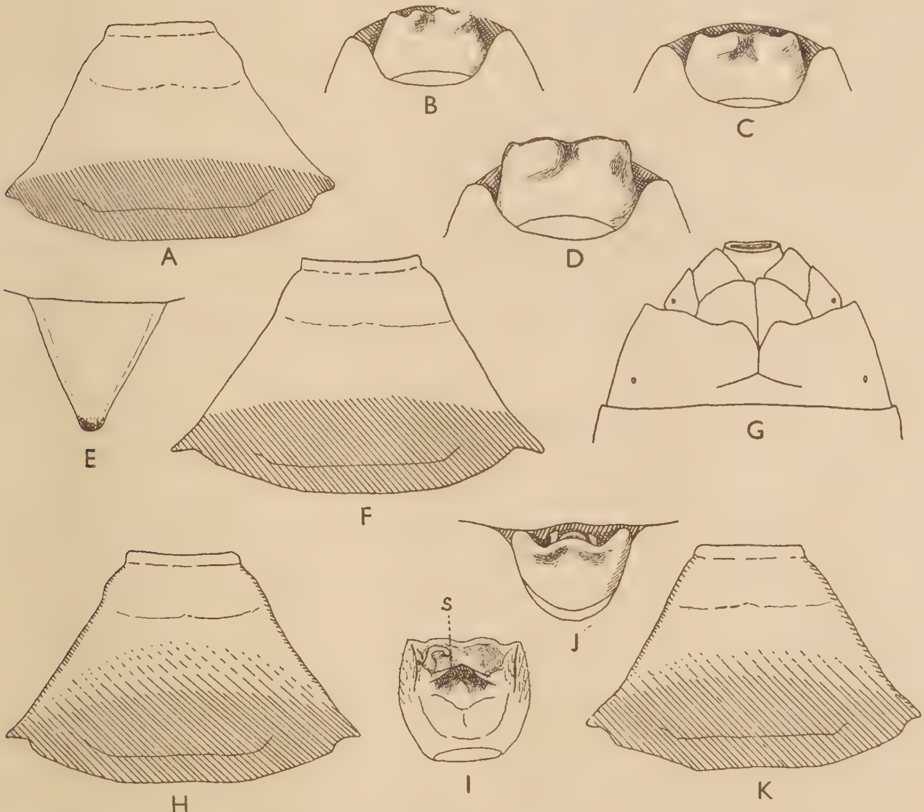

Fig. 10.—*Amblypelta cocophaga cocophaga* China: (A, H, K) pronotum (from Guadalcanal, Kolombangara and New Georgia, respectively); (B, C) tip of ♂ abdomen, ventral view (from Guadalcanal and Rendova, respectively); (J) the same in rear view (Guadalcanal); (E) scutellum (Guadalcanal); (G) tip of ♀ abdomen, ventral view (Guadalcanal).
Amblypelta cocophaga malaitensis, subsp.n. (Malaita): (D) tip of ♂ abdomen, ventral view; (F) pronotum; (I) ♂ pygophore from above, with left paramere and rectum removed (S, " shelf ").

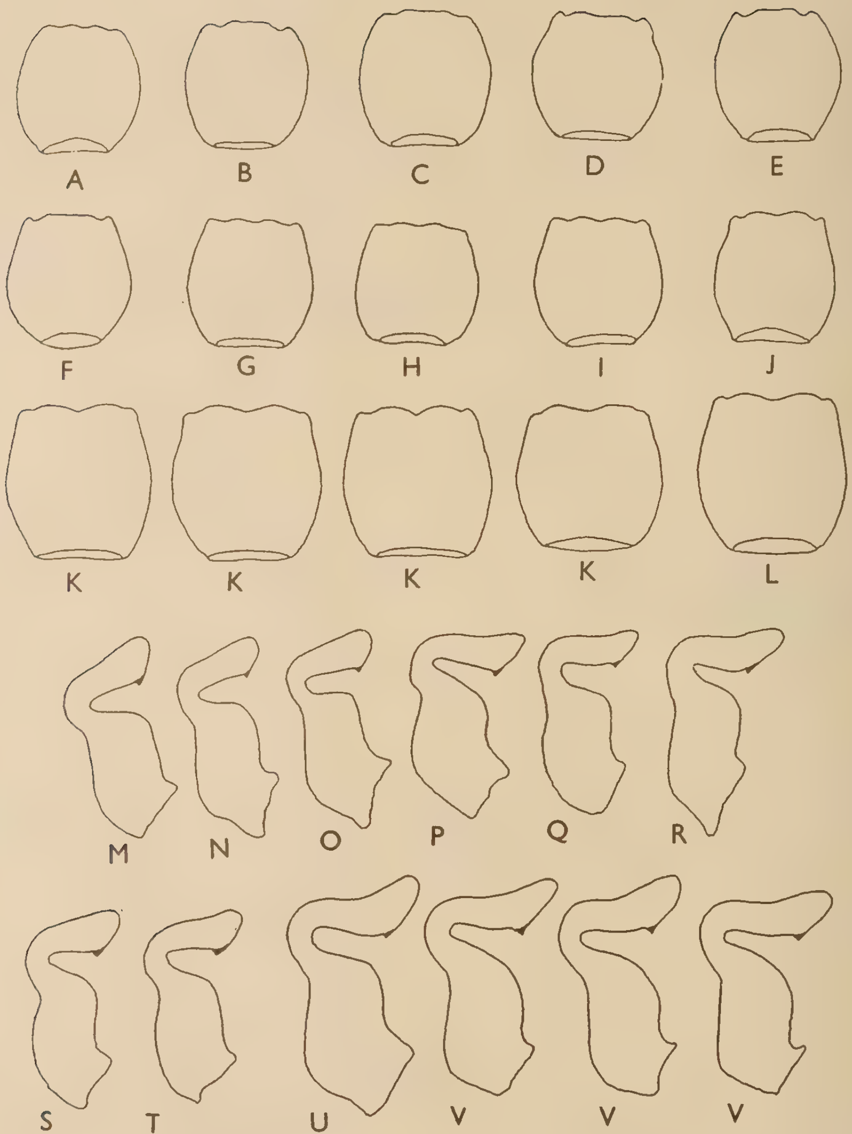

Fig. 11.—*Amblypelta cocophaga* China: top three rows, ♂ pygophore from below, in outline; lower two rows, left paramere, inner view; in outline.
Amblypelta cocophaga cocophaga China: (A–D) from Guadalcanal (specimens from Kukum, Gold Ridge, Sutakiki R., Takanboru); (E–F) from Nggela (specimens from Bungana and Sambani); (G–J) from Western Group (specimens from Kolombangara, New Georgia, Rendova, Wana Wana); (M–O) from Guadalcanal (specimens from Gold Ridge, Takanboru, Kukum); (P–R) from Western Group (specimens from Rendova, Wana Wana, Kolombangara); (S–T) from Nggela (specimens from Bungana and Sambani).
A. cocophaga malaitensis, subsp.n. (from Malaita): (K, V) specimens from Baunani; (L, U) from Malu'u.

Islands, but insufficient to recognise any further subspecies; this variation is best described after treatment of the Malaita subspecies (p. 530).

The following biometrical details of the type form supplement China's description.

Pronotum with moderately developed anterior collar; broader than long as 67 : 45. Scent gland with posterior lobe of the peritreme more than half as long as the aperture (11 : 18). *Scutellum* about as broad as long; breadth : length as 28 : 26, in some specimens as 25 : 24 and 31 : 26; surface coarsely punctate, slightly transversely rugose. *Hemelytra* with cell *m-cu* rhomboidal, usually divergent posteriorly. *Antennae* longer than head and body combined by 2·0–3·0 mm. in males, and 0·3–2·5 mm. in females; ratio of segments I–IV as 60 : 70 : 44 : 60 in male, 64 : 70 : 46 : 58 in female (these are subject to variation, however). *Rostrum* of variable length, reaching to the middle of the posterior acetabula in some specimens, to the middle of the 2nd abdominal segment in others; ratio of segments I–IV as 28 : 23 : 16 : 28.

Length, 13·0–14·0 (♂), 14·5–16·0 mm. (♀); width across humeral angles, 4·0–4·4 mm. (♂), 4·5–5·1 mm. (♀).

Distribution.

There are too many records to give full details as for other species: total numbers of specimens examined and localities only will be given.

GUADALCANAL: 87 ♂♂, 65 ♀♀ from Aruligo, Berande, Gold Ridge (2–3,000 ft.), Koilotumaria, Kokumbona, Kukum, Matanikau, Rua Vatu, Suta (2,000 ft.), Sutakiki River (2–3,000 ft.), Takanboru, Tenaru, Tenavatu, Toni River. The most interesting records are those from high altitudes in the forest; Suta and the Sutakiki River are approximately in the centre of the island. In the Bishop Museum, Honolulu, is a single ♂ labelled "Guadalcanar, 12–20 (*J. A. Kusche*)"; this is probably the earliest specimen to be collected. NGGELA: 11 ♂♂, 6 ♀♀ from Bungana, Sambani; also 5 ♂♂ from Tulagi (*R. J. A. W. Lever*, 1933–4). NEW GEORGIA: 8 ♂♂, 9 ♀♀ from Banga, Pauru and Sasavele. RENDOVA: 5 ♂♂, 3 ♀♀ from main island, and from Ugeli. GANONGA: 1 ♂, Koreovuku (*R. J. A. W. Lever*, 1936). KOLOMBANGARA: 11 ♂♂, 13 ♀♀ from Gatere (*J. Holsheimer*), Kuzi, and unspecified locality (*E. A. Armytage*, 1922). BOUGAINVILLE: 1 ♂, 1 ♀ from Buka (Gagan) and Kokorei (*J. L. Gressitt*).

Specimens are deposited in A, B, L, PM, SA, SI.

The various host-plants of this form and the ssp. *malaitensis* are too numerous to mention here, but will be listed in a separate publication.

Amblypelta cocophaga malaitensis, subsp.n.

Amblypelta cocophaga, China (1934, p. 187) (part).

A. cocophaga from all Malaita localities appear to differ consistently from the type form in the following characters:—

Male pygophore: the pygophore is much larger, extending beyond the 9th tergum and tapering much less strongly at the posterior end so that it is more parallel-sided and the posterior margin, which is often deeply pigmented, is much broader (figs. 10 D, I, 11 K, L). In the type form it is smaller and more tapered posteriorly (figs. 10 B, 11 A–F).

Male parameres: the parameres have the outer side of the distal arm concave (figs. 11 U, V, 16 H); in the type form it is usually more or less straight or only slightly concave, and the tip is more broadly rounded (figs. 11 M–O, S, T, 16 G).

Pronotum: the humeral angles are more acuminate, and produced (fig. 10 F).

Elytra: darker, of a dull chocolate brown, not castaneous as is usual in the type form.

Antennae: segment IV is less pigmented; the infuscate terminal part is

usually feebly pigmented and confined to the tip (fig. 17 E); in the type form it is deeply pigmented and comprises about half the segment (fig. 17 F).

In other details this subspecies resembles the type form.

Length, 12·1–14·5 mm. (♂), 15·1–16·2 mm. (♀); width across humeral angles, 4·1–4·8 mm. (♂), 5·1–5·2 mm. (♀).

In smaller specimens the subspecific structural characters tend to be less well marked than in larger ones.

Distribution.

Malaita: 26 ♂♂, 23 ♀♀ and upwards of 500 unsexed adults from Auki, Baunani, Fulisago, Hulo, Malu'u, Nafinua, Rai'ako, Rongofano, Saote and Su'u. Collections from Fulisago, Rai'ako and Saote show that this subspecies occurs in forest areas right through the island, in the same way that the type form does on Guadalcanal.

Specimens are deposited in A, B, H, L, PM, SA, SI.

The Western Islands form of A. cocophaga.

The Malaita form might well be regarded as a good species were it not for the fact that specimens from the Western Islands (Kolombangara, New Georgia, Rendova, etc.) are to some extent intermediate between typical ssp. *cocophaga* and ssp. *malaitensis*. The male pygophore is somewhat less tapered than in *cocophaga* (fig. 10 C, fig. 11 G–J); the paramere has the outer side of the distal arm slightly more convex (fig. 11 P–R); the colour pattern of antennal segment IV is usually intermediate; the differences are slight, but tend to bridge the gap. The western forms usually differ also in a colour character; the pronotum is more heavily pigmented than in either typical *cocophaga* or *malaitensis*, the darkened posterior part extending further forward and shading gradually into the pale anterior part (fig. 10 H, K); this character is not consistent, however, and it seems best to include the western forms in with the typical subspecies from Guadalcanal and Nggela.

The only two specimens from Bougainville are small (♂ 13·0 mm., ♀ 13·1 mm.); in colour pattern they resemble the typical ssp. *cocophaga* rather than the Western Islands form; in the pygophore the male is intermediate between ssp. *malaitensis* and the type form.

Amblypelta costalis costalis Van Duzee.

Amblypelta costalis, Van Duzee (1940, p. 180).

There is little to add to the full original description given by Van Duzee; a few details only will be mentioned for ready comparison with the other descriptions in this revision.

Colour. This subspecies differs from most other members of the genus by the general body colour when fresh, which is testaceous or yellowish testaceous with little trace of green; this character is of no value in dried specimens. The black subcostal stripe on the hemelytra is longer than in *A. cocophaga*, but less clearly defined and less intensely black. The chestnut-brown basal band on the pronotum is broad in the centre, its anterior border convex (fig. 12 A).

Pronotum with a feebly developed anterior collar (fig. 12 A); humeral angles acute and fairly prominent; scent gland with posterior lobe of the peritreme about half the length of the aperture. *Scutellum* with the truncate tip usually slightly emarginate (fig. 12 D). *Hemelytra* with cell *m-cu* slightly rhomboidal, slightly divergent posteriorly. *Antennae* about 1·5–2·0 mm. longer than head and body in males; not more than 1·0 mm. longer, and sometimes slightly shorter, in females. Ratio of segments I–IV as 56 : 68 : 46 : 57 in males, and as 58 : 69 : 45 : 51 in females; IV is therefore about equal to I in males, shorter in females (fig. 17 G). *Rostrum* with segments I–IV as 27 : 24 : 18 : 31 (♂).

Male: pygophore characteristic, with v-shaped emargination in posterior margin as seen ventrally (fig. 12 C), and broadly and shallowly u-shaped in posterior view (fig. 12 B). Parameres curiously twisted (fig. 16 M, N).

Female: transverse fissure of VIIth abdominal segment obtusely angled or somewhat rounded in the centre, the sternum anterior to it and at its lateral ends characteristically raised to form a transverse ridge (fig. 12 E).

Length, 13·0–14·0 mm. (♂), 14·3–15·6 mm. (♀); width across humeral angles, 4·6–4·75 mm. (♂), 5·0–5·25 mm. (♀).

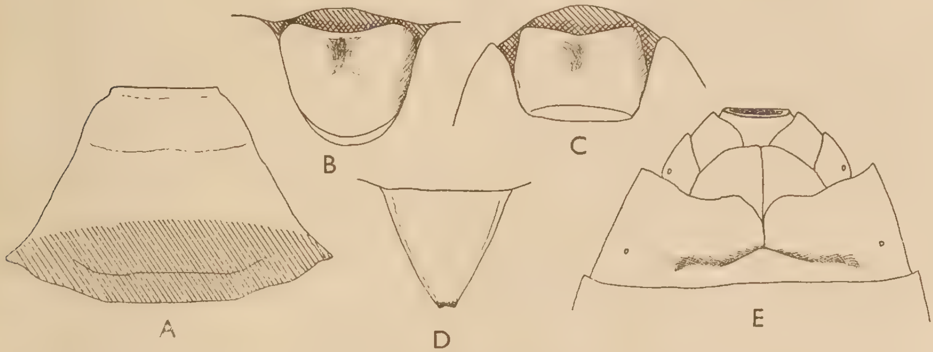

Fig. 12.—*Amblypelta costalis costalis* Van Duzee: (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum; (E) tip of ♀ abdomen, ventral view.

Distribution.

Bellona: Gotokanamba, 20.xi.1955, 7 ♂♂, 7 ♀♀; 21.xi.1955, 8 ♂♂, 7 ♀♀; Tahanuku, 21.xi.1955, 17 ♂♂, 8 ♀♀; all on *Manihot esculenta*; other specimens taken on *Carica papaya*. Larvae were taken with adults.

Specimens are deposited in L, PM, SA, SI.

Amblypelta costalis szentivanyi, subsp.n.

This subspecies, from New Guinea and the Bismarck Archipelago, comes very close to the type form from Bellona, and is with difficulty distinguished in some specimens. In general structure and coloration it is similar (see fig. 13). It

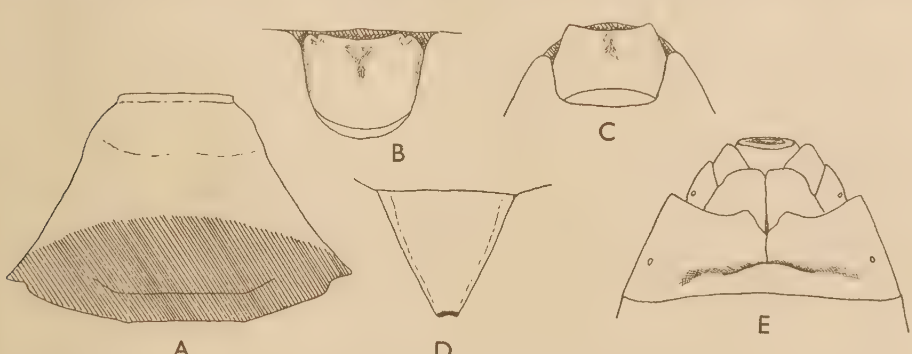

Fig. 13.—*Amblypelta costalis szentivanyi*, subsp.n.: (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum; (E) tip of ♀ abdomen, ventral view.

differs in the male hypopygium, which has the posterior lateral angles more pointed and the lateral margins more convergent posteriorly (fig. 13 C); viewed from behind, there is usually a small "notch" or groove in each side of the emargination of the posterior border (fig. 13 B) which is rarely present in the type form. These characters, however, are variable. Parameres strongly twisted (fig. 16 O, P).

Antennae: 1·5–3·0 mm. longer than head and body in males, 0·5–1·3 mm. longer in females; ratio of segments I–IV as 61:72:48:63 in males (fig. 17 I), and as 61:70:47:55 in females. *Rostrum* of the same length as in the type form, the ratio of segments I–IV as 25:24:19:31.

Length, 13·0–14·1 mm. (♂), 15·3–15·8 mm. (♀); width across humeral angles, 4·1–4·6 mm. (♂), 4·6–5·1 mm. (♀).

Distribution.

Papua, New Guinea: Mt. Lamington, i.1929, 1 ♀ (*C. T. McNamara*); Popondetta, 20.iii.1956, 2 ♂♂, on *Manihot esculenta*; Sangara, Popondetta, 21–22.iii.1956, 10 ♂♂, 9 ♀♀, larvae on *Hevea brasiliensis*; 22–23.iii.1956, 2 ♂♂, 3 ♀♀, larvae, on *Manihot esculenta*. New Britain: Keravat, 1956, 1 ♂, on *Theobroma cacao* (*G. S. Dun*); 30–31.iii.1956, 3 ♂♂, 6 ♀♀, on *Manihot esculenta* (up to an altitude of 1,000 ft.). New Ireland: Gilingil, 7.v.1956, 1 ♀, 1 larva (*J. L. Gressitt*).

Specimens have been deposited in PM, SI.

The New Ireland record is based on only one female, so that the subspecies is in doubt, but it is placed here provisionally until more material can be studied.

The conspecificity of this form from Papua with those from Rennell and Bellona is of considerable zoogeographical interest, and will be discussed later.

Amblypelta costalis rennellensis, subsp.n.

All the specimens obtained on Rennell Island differ from those from Bellona in the following characteristics:—

Colour: general body colour distinctly green when fresh rather than yellowish.

Rostrum: relatively longer, reaching the posterior margin of the 2nd abdominal (1st ventral) segment, while in the Bellona subspecies it only reaches the middle of this segment; ratio of segments I–IV as 25:23:17:30 (♂).

Antennae: distinctly shorter than head and body in females, slightly longer in males. Ratio of segments I–IV as 44:54:38:53 in males, and as 46:55:39:46 in females: thus IV is equal to I in females, and distinctly longer than I in males (fig. 17 H) (in *A. costalis costalis* it is equal in males and shorter in females).

Size: length, 11·5–12·7 mm. (♂), 13·0–13·8 mm. (♀); width across humeral angles, 3·9–4·2 mm. (♂), 4·4–4·7 mm. (♀); thus it is much smaller than the type form of the species, and sex for sex there is no overlap.

These differences seem to be quite clear-cut and reasonably constant, but do not justify the erection of anything more than a subspecies.

Distribution.

Rennell: Lavanggu, 23.xi.1955, 1 ♂, 1 ♀, on *Carica papaya* and *Merremia tuberosa*; 24.xi.1955, adult and larvae on shrub (Rubiaceae); 30.xi.1955, 1 ♂ (holotype), 1 ♀, on *Merremia tuberosa*; Matange, 24.xi.1955, 1 ♂, 1 ♀, on *Manihot esculenta*; 30.xi.1955, 12 ♂♂, 10 ♀♀ on *Manihot esculenta*; Vaitahi, 29.xi.1955, 3 ♂♂, 2 ♀♀, on unknown climbing plant. Larvae were found with adults on most occasions.

Specimens have been deposited in PM, SI.

A single female from Misima I., Papua, which is near the eastern end of the Louisiade Archipelago, is clearly related to and probably conspecific with *A. costalis*; the antennal ratio (I–IV as 54:60:40:59) is somewhat different from

any known subspecies, but in the absence of males it is not advisable to give it a name.

Another single female specimen from Dutch New Guinea (Araucaria Camp, 800 metres, collected by *L. J. Toxopeus*, 19.iii.1939), in the Leiden Museum of Natural History, appears to be related to *A. costalis*, but is smaller than the type form (length 13·3 mm.), has a shorter pronotum and much shorter and more slender antennae and legs; it appears to be specifically distinct, but more material would be necessary to describe it.

Amblypelta gallegonis gallegonis Lever.

Amblypelta gallegonis, Lever (1936, p. 324).

This species is so distinct, with its orange-yellow and metallic greenish-black coloration and entirely black scutellum, that little need be added to Lever's description; details will be confined mainly to additional structural features.

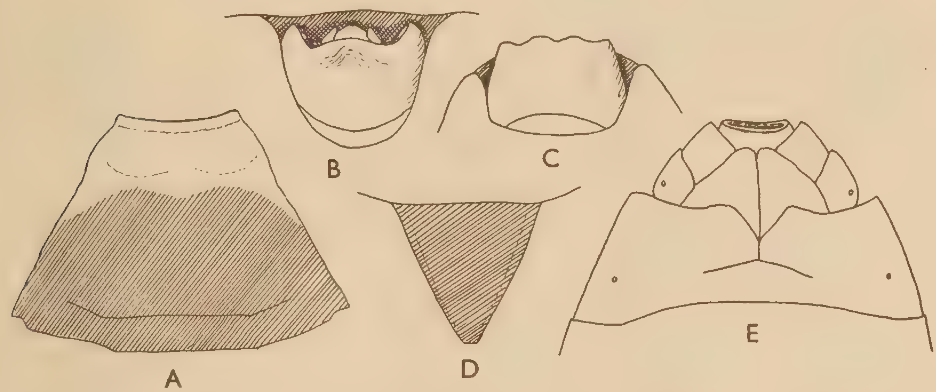

Fig. 14.—*Amblypelta gallegonis gallegonis* Lever: (A) pronotum; (B) tip of ♂ abdomen, rear view; (C) the same in ventral view; (D) scutellum; (E) tip of ♀ abdomen, ventral view.

Colour. The following detail is of importance as a subspecific character: thoracic pleura yellow, with vertical black bands at the posterior margins of the segments, which broaden dorsally and usually form a continuous black longitudinal fascia (fig. 15 A).

Pronotum broader than long as 3:2; side margins nearly straight; humeral angles acute, but not prominent (fig. 14 A); anterior collar fairly well marked;

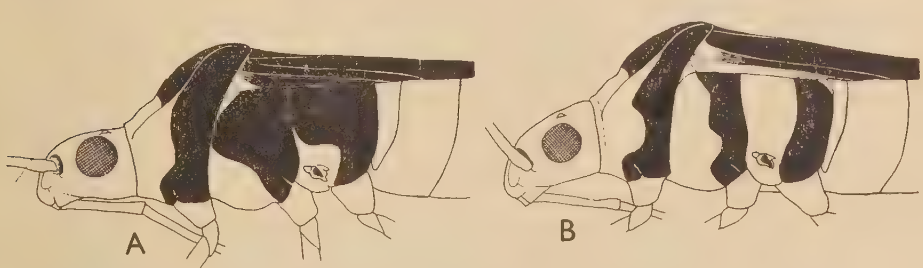

Fig. 15.—Head and thorax from left side (showing colour pattern) of *Amblypelta gallegonis gallegonis* Lever (A), and *A. gallegonis bougainvillensis*, subsp.n. (B).

anterior lobes smooth, unpunctured, posterior part coarsely and deeply punctured. Scent gland with posterior lobe of peritreme about $\frac{2}{5}$ as long as the aperture. *Scutellum* as broad as long, or very slightly broader; the tip squarely or sometimes roundly truncate (fig. 14 D); the surface coarsely punctured, and transversely rugose across the middle. *Hemelytra* with cell *m-cu* rhomboidal, slightly divergent posteriorly. *Antennae* long, about 4–6 mm. longer than head and body combined in males, 2–4 mm. longer in females; ratio of segments I–IV as 71:81:51:75 in males, 73:88:55:74 in females (fig. 17 A). *Rostrum* reaching the middle or the hind border of the posterior acetabulum; ratio of segments I–IV as 27:23:17:30.

Male: pygophore as in fig. 14 B, C, the posterior margin sinuate in rear view; parameres characteristic (fig. 16 Q).

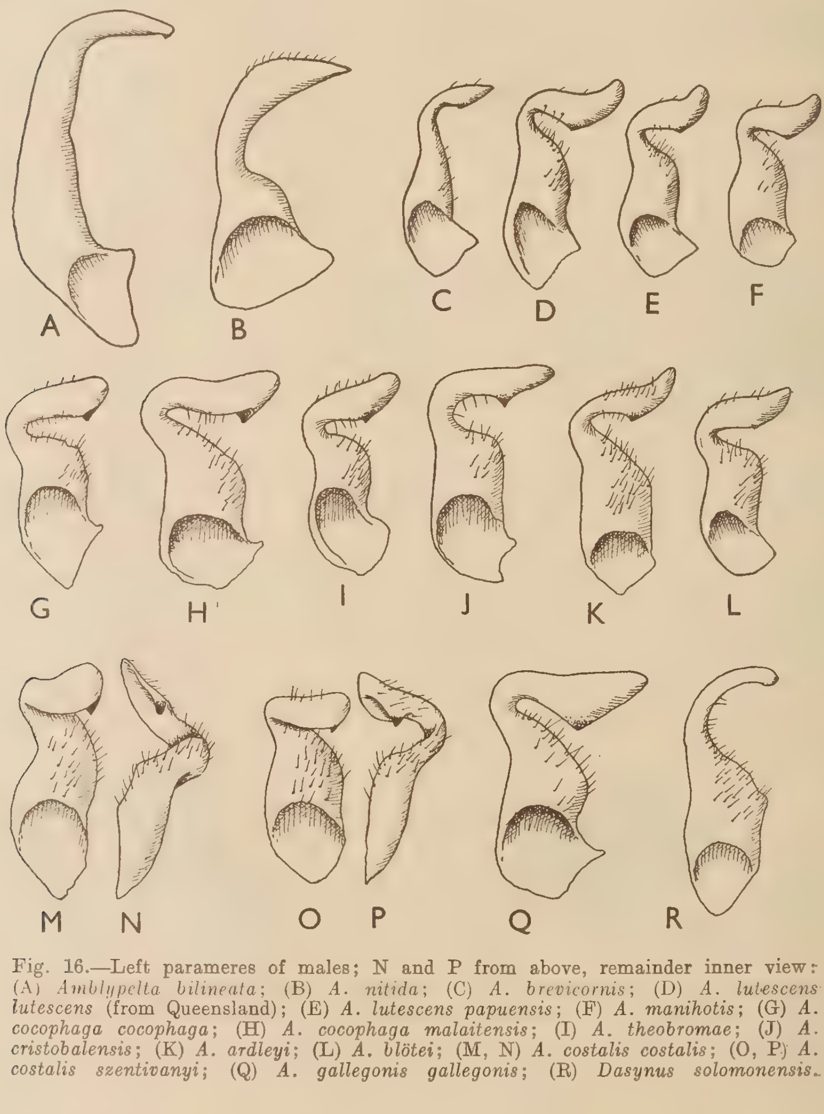

Fig. 16.—Left parameres of males; N and P from above, remainder inner view: (A) *Amblypelta bilineata*; (B) *A. nitida*; (C) *A. brevicornis*; (D) *A. lutescens lutescens* (from Queensland); (E) *A. lutescens papuensis*; (F) *A. manihotis*; (G) *A. cocophaga cocophaga*; (H) *A. cocophaga malaitensis*; (I) *A. theobromae*; (J) *A. cristobalensis*; (K) *A. ardleyi*; (L) *A. blötei*; (M, N) *A. costalis costalis*; (O, P) *A. costalis szentivanyi*; (Q) *A. gallegonis gallegonis*; (R) *Dasynus solomonensis*.

Female: transverse fissure on the VIIth abdominal sternum angled in the middle, not sinuate (fig. 14 E).

Length, 14·0–15·2 mm. (♂), 15·5–16·2 mm. (♀); width across humeral angles, 4·1–4·25 mm. (♂), 4·6–5·25 mm. (♀).

Distribution.

YSABEL, BRITISH SOLOMON ISLANDS: Buala, Maringe Lagoon, 8–9.ii.1955, 4 ♂♂, 1 ♀, 5 larvae; Holokama, Maringe Lagoon, 17.ii.1956, 2 ♂♂, 1 ♀, 1 larva; 21.ii.1956, 1 ♂, 1 larva; Sisaga, 20.ii.1956, 6 ♂♂, 3 ♀♀, 1 larva; all on *Manihot esculenta*. Previously recorded by Lever from Fulakora and Pele on the same island.

Specimens have been deposited in PM, SI.

Amblypelta gallegonis bougainvillensis, subsp.n.

Resembles *A. gallegonis gallegonis* in all features except colour; it is paler, especially the thoracic pleura, on which the vertical black stripes at the posterior margins of the segments are narrow, linear, not broadening nor coalescing dorsally. This feature is consistent in all specimens studied (fig. 15 B), except for 3 specimens from Buka (see below).

Length, 14·2–15·0 mm. (♂), 15·0–16·4 mm. (♀); width across humeral angles, 4·3–4·35 mm. (♂), 4·5–5·2 mm. (♀).

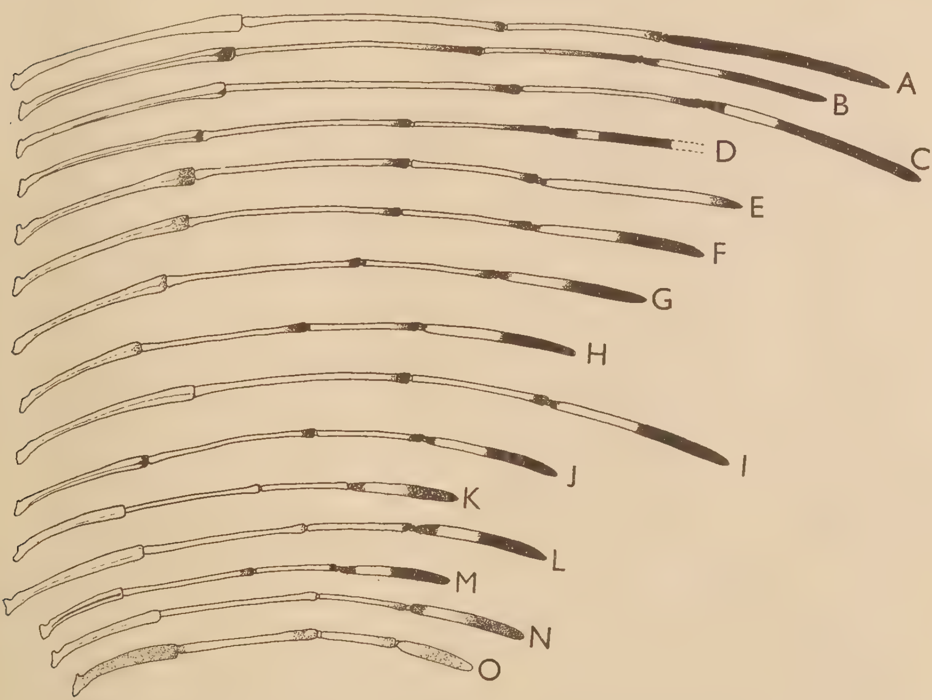

Fig. 17.—Antennae of males: (A) *Amblypelta gallegonis gallegonis*; (B) *A. theobromae*; (C) *A. ardleyi*; (D) *A. blötei*; (E) *A. cocophaga malaitensis*; (F) *A. cocophaga cocophaga*; (G) *A. costalis costalis*; (H) *A. costalis rennellensis*; (I) *A. costalis szentivanyi*; (J) *A. cristobalensis*; (K) *A. lutescens lutescens* (from Queensland); (L) *A. lutescens papuensis*; (M) *A. bilineata*; (N) *A. nitida*; (O) *A. brevicornis*.

Distribution.

Choiseul, British Solomon Islands: Taura, 27.iii.1957, 3 ♂♂, 1 ♀; Posarai, 31.iii.1957, 2 ♀♀; Sasamuga, 1.iv.1957, 2 ♂♂, 1 ♀; Voza, 4.iv.1957, 2 ♂♂, 2 ♀♀; Luti, 28.iii. 1957, larvae; larvae taken at all stations; all collected from *Manihot esculenta* by *P. G. Fenemore*. Bougainville: Numa-Numa, 29.viii.1922, 1 ♂ (*E. A. Armytage*); iv.1956, 1 ♂, 3 ♀♀ (*C. Sandford*); 31.v.1956, 2 ♂♂, 4 ♀♀, on *Manihot esculenta*; 1–2.vi.1956, ♂ holotype and 11 ♂♂, 11 ♀♀, larvae, on *Ipomoea alba*, *Piper* sp., *Pueraria phaseoloides*; Kieta, v.1934, ii.1935 and x.1937, 2 ♂♂, 1 ♀ (*J. L. Froggatt*); 30.v.1956, 1 ♂, 6 ♀♀, 2 larvae, on *Manihot*; Buin, 21.vii.1922, 1 ♂ (*E. A. Armytage*); 1.vi.1956, 1 ♀, on *Manihot* (*J. L. Gressitt*); Sovele, 6.vi.1956, 1 ♀ (*J. L. Gressitt*); Kokorei, 8–9.vi.1956, 4 ♀♀, on *Manihot* (*J. L. Gressitt*); Buka, Gagan, 15.vi.1956, 1 ♂, 2 ♀♀ (*J. L. Gressitt*); Boku, 4–5.vi.1956, 1 ♂, 2 ♀♀, on *Manihot* (*J. L. Gressitt, E. J. Ford*); Kokure, 690 metres, 9.vi.1956, 2 ♂♂, on *Ipomoea batatas* (*E. J. Ford*); 11.vi.1956, 6 ♂♂, 1 ♀ (*E. J. Ford*); Mosigeta, 3.vi.1956, 1 ♀ (*E. J. Ford*); Simba Mission, 1.vii.1956, 1 ♀ (*E. J. Ford*); Bougainville, 1 ♂, 2 ♀♀ (Rev. *A. H. Voyce*) (SA).

Specimens have been deposited in B, PM, SI.

This subspecies evidently replaces the type form completely on Choiseul and Bougainville. The three specimens from Buka I., at the west end of Bougainville but almost connected with it, all differ from those from the mainland in having the black lateral thoracic stripes suppressed altogether; it is not worth raising another subspecies for this form unless it is shown to be consistent in more material from Buka.

Dasynus solomonensis, sp.n.

This species is described in this paper because a closely related species was described in *Amblypelta* as *A. fumosa* Blöte; the latter is here transferred to *Dasynus*, and with the available material of the new species here described the reasons for doing so will be the more easily appreciated.

Colour and punctuation. Hemelytra blackish brown, or brown with the punctures darker; the veins on the hind part of the corium tending to be paler; membrane black. Pronotum with anterior lobe and collar pale brown, the posterior part darker, sometimes abruptly dark, almost black, sometimes becoming gradually darker posteriorly; humeral angles black, this colour extending along the lateral carinae onto the anterior collar (fig. 18 E). Scutellum varies from entirely yellowish brown to black, with the tip yellow. Head yellowish brown with a dark spot at the posterior border of each ocellus. Underside pale brown, with a dark spot on each side of the three thoracic segments and of abdominal segments II–V (in one specimen II–III only). Antennae dark brown, the tips of segments II and III, distal $\frac{2}{3}$ and base of IV darker. Legs uniformly brown, darker in some specimens, paler in others. Puncturation fairly dense and deep on pronotum and hemelytra.

Head shorter than pronotum as 31:51. Ocelli slightly closer to the eyes than to the median line of the head. Bucculae deepest at the anterior angles, which are obtuse and very broadly rounded. Tylus porrect, well produced anteriorly. *Pronotum* broader than long as 73:51; side margins straight or slightly concave in the posterior part; humeral angles acute but not prominent; anterior collar strongly developed (fig. 18 E). Scent gland with posterior lobe of peritreme more than half as long as the aperture (13:20). *Scutellum* about as wide as long (31:32), slightly rounded, not truncate apically (fig. 18 H); coarsely punctate, and rather strongly transversely rugose in holotype, less so in other specimens. *Hemelytra* with cell *m-cu* rhomboidal, broad and rather strongly divergent posteriorly. *Antennae* long and slender, slightly longer than head and body combined; ratio of segments I–IV as 64:70:56:95 in male, 64:74:60:93 in female;

segment IV is by far the longest. *Rostrum* long, reaching the posterior margin of the 3rd abdominal segment; ratio of segments I–IV as 32:35:24:50.

Male: pygophore with a central prominence on the posterior margin and a deep emargination on each side of it (fig. 18 F, G); central cavity with a triangular transverse partition or "shelf". Parameres as in fig. 16 R, the distal arm evenly curved, slender throughout, unarmed.

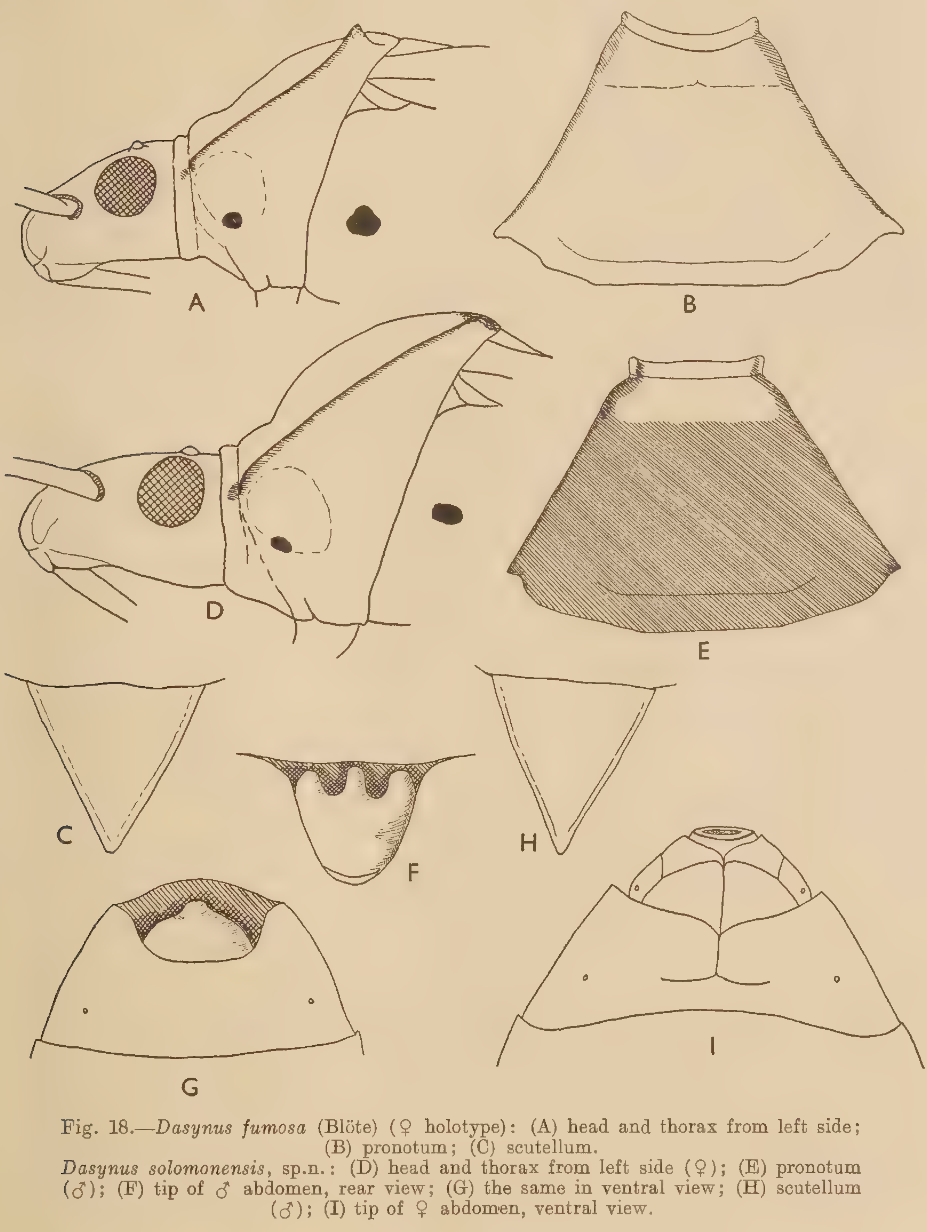

Fig. 18.—*Dasynus fumosa* (Blöte) (♀ holotype): (A) head and thorax from left side; (B) pronotum; (C) scutellum.
Dasynus solomonensis, sp.n.: (D) head and thorax from left side (♀); (E) pronotum (♂); (F) tip of ♂ abdomen, rear view; (G) the same in ventral view; (H) scutellum (♂); (I) tip of ♀ abdomen, ventral view.

Female: transverse fissure of the VIIth abdominal sternum obtusely angulate, slightly sinuate (fig. 18 I).

Length, 15·0–17·0 mm. (♂), 19·5 mm. (♀); width across humeral angles, 4·4–5·4 mm. (♂), 6·15 mm. (♀).

Distribution.

GUADALCANAL, SOLOMON ISLANDS: Lunga River, 15.v.1937, 1 ♂ (*W. Cottrell-Dormer*); Kukum, 3.iv.1956, 2 ♂♂ (including holotype), 1 ♀, on *Amoora* sp. (a forest tree).

One specimen has been deposited in SI.

This species differs from *D. fumosa* (Blöte) (described from a single ♀), in being larger, and in the pronotum, which has the disc more convex, the humeral angles less prominent, and the colour much paler (fig. 18 A, B, D, E).

Generally, *D. solomonensis* differs from *Amblypelta* in the following characters:—(i) scutellum not truncate, (ii) male parameres unarmed and not dilated apically (as in all larger species of *Amblypelta*), (iii) in the larvae, which have the antennal segments simple, somewhat flattened but not broadly dilated as in *Amblypelta* species (see Phillips, 1940, figs. 2 & 3), and (iv) in egg-laying habits; in all *Amblypelta* species in which they are known the eggs are laid singly; in *D. solomonensis*, 46 eggs were laid in a group of close-set, parallel rows.

Zoogeographical Considerations.

The genus *Amblypelta* as here defined, and as known so far, is confined to Australia north of Sydney, the islands between Australia and New Guinea, New Guinea and, to the west, the Kai Is., Timor and Java; the Bismarck Archipelago (New Britain and New Ireland); the Solomon Islands including Bougainville, Rennell and Bellona; the New Hebrides and New Caledonia. The western limit is interesting in that it extends beyond " Wallace's Line " (see Newbigin, 1950, pp. 234–236, for a discussion of this).

From zoogeographical and taxonomic standpoints the genus can conveniently be divided into the following groups.

(i) *A. bilineata*, *A. nitida* and *A. brevicornis*. These are taxonomically distinct from the remainder in the structure of the hypopygium (lacking a transverse partition or " shelf " across the internal cavity), the parameres, and the transverse fissure of the female VIIth sternum, which is sinuate and scarcely angled in the middle; the first two at all events are obviously closely related. They occur in the New Hebrides, New Caledonia and the southern part of the range of the genus in Australia. It should be mentioned here that a single larva was collected in the New Hebrides, near Vila, of what appears to be one of the larger species such as those found in New Guinea and the Solomon Islands, rather than *A. bilineata* which alone has been found there in the adult stage.

(ii) *A. lutescens* and *A. manihotis* are annectant between the foregoing and the larger species further north, not only geographically but morphologically. They resemble the former in the lack of a pronotal collar, the latter in the form of the male paramere, and are intermediate in the male pygophore (in which the " shelf " is present but not well developed) and in the transverse fissure of the female VIIth sternum, which is slightly sinuate. They have a wide range from northern Australia to southern New Guinea and the islands between, as far west as Java.

(iii) The northern group of usually larger species from New Guinea, the Bismarcks and the Solomon Islands have a more or less well developed pronotal collar, a characteristically elbowed male paramere with a rounded tip and subapical

tooth, a well-developed "shelf" across the hypopygial cavity, and a more or less sharply angled transverse fissure, with straight non-sinuate arms, on the female VIIth abdominal segment. Within this group are the following: (a) *A. costalis*, a polytypic species with subspecies in Papua (and the Bismarcks), Bellona and Rennell (but not in the main Solomon Islands); (b) three species of more limited range in New Guinea (*theobromae*, *ardleyi* and *blötei*); (c) two quite distinct polytypic species in the Solomon Islands, namely *A. cocophaga*, of which *A. theobromae* appears the closest relative, and *A. gallegonis* which is quite distinct from any other, especially in the male paramere; (d) *A. cristobalensis*, confined to San Cristobal at the eastern end of the Solomon Islands and probably derived as an off-shoot of *A. cocophaga*.

A. costalis is of great interest, since it is another example of affinity of the islands of Rennell and Bellona with New Guinea (through the Louisiade Archipelago) rather than with the main islands of the Solomons group; such affinity has been previously found in butterflies (Carpenter, 1953); in fact, *A. costalis costalis* from Bellona shows greater resemblance to *A. c. szentivanyi* from Papua and the Bismarcks than it does to *A. c. rennellensis* from the closely adjacent Rennell I.

The two Solomon Islands species, *A. cocophaga* and *A. gallegonis*, have an interesting distribution in that they do not apparently co-exist on the same islands except for Bougainville at the western end, where *gallegonis* (subsp. *bougainvillensis*) is common and *cocophaga* apparently rare; from Bougainville *gallegonis* extends down the northern chain of islands through Choiseul as far as Ysabel, while *cocophaga* extends down the southern chain through New Georgia and the adjacent western islands to Guadalcanal, Nggela and then, curiously, across to Malaita in the northern chain. The fact that the Malaita population has developed subspecific characters, and the San Cristobal population has become specifically distinct, indicates that this distribution came into being a long time ago. Another curious fact is that in the Russells group, between New Georgia and Guadalcanal, *Amblypelta* appears to be altogether absent; it must have occurred there at some stage in the history of the genus, and for some unknown reason died out since; otherwise the existing distribution would scarcely be accountable.

It therefore appears that *Amblypelta* species in the Solomon Islands have acquired their present distribution by three parallel routes; *A. gallegonis* through the northern chain of islands, *A. cocophaga* through the southern chain, and *A. costalis* from New Guinea through the Louisiade Archipelago to Rennell and Bellona. In each of these lines of infiltration, subspeciation has occurred as a result of fragmentation of the island chains, and in the case of *A. cocophaga* one fragment has evolved specific status in the form of *A. cristobalensis*.

A point of interest arising from inter-island distribution within the Solomon Islands is the effectiveness of the barrier provided by quite narrow channels of sea. The distance between Guadalcanal and San Cristobal is only 40 miles, yet the fact that their *Amblypelta* populations have become specifically distinct indicates that they have been in mutual isolation for a very long time. Similarly, the Malaita population has become subspecifically but clearly distinct from that on Nggela, only 27 miles away. There has been no exchange of populations between *gallegonis* on Ysabel and *cocophaga* on Malaita (47 miles apart); nor has *cocophaga*, assuming that it died out in the Russell Islands, managed to re-establish itself from Guadalcanal, only 20 miles distant. Although most species take wing very readily and appear to fly strongly, they evidently do not undertake flights of any great distance. It is important to realise this, and to take any necessary measures to ensure, in the interests of preventing the spread of the important pests within the genus, that their inability to spread from one island to another by natural means is not nullified in some way by accidental human transport.

Summary.

In view of the discovery of several new species and subspecies of *Amblypelta* (Hemiptera, Coreidae), some of which are either known to be or else threaten to become of economic importance, a revision of the whole genus has become necessary.

The genus *Amblypelta*, as defined in the present paper and as known so far, is confined to Australia north of Sydney, the islands between Australia and New Guinea, New Guinea and, to the west, the Kai Is., Timor and Java; the Bismarck Archipelago, the Solomon Islands including Bougainville, Rennell and Bellona; the New Hebrides and New Caledonia. In the present revision of the genus, twelve species and five subspecies are included, of which all but seven species are new to science. Apart from the descriptions of the new species and subspecies, taxonomic notes on the previously known species are given as well as a key to all the species.

The known distribution of each species is stated, and consideration given to the zoogeography of the genus as a whole, and of certain species-groups which can be recognised within the genus.

Acknowledgements.

I wish to express my thanks to G. S. Dun, Dr. J. J. H. Szent-Ivany and J. H. Ardley for sending material for study from New Guinea and New Britain and providing facilities for further collecting during my visits to those territories; Dr. J. L. Gressitt for material from Bougainville and New Ireland; C. P. Hoyt and F. Cohic for specimens of *Amblypelta bilineata* from New Caledonia, and for information; Prof. R. L. Usinger for a type specimen of *A. costalis*. For the loan of material for study from various collections, I am indebted to the following: C. E. Chadwick (N.S.W. Department of Agriculture), T. G. Campbell (C.S.I.R.O., Canberra); Dr. H. C. Blöte (Rijksmuseum van Natuurlijke Historie, Leiden); the Directors of the Hungarian National Museum (Budapest), the Naturhistoriska Riksmuseum (Stockholm), the Australian Museum (Sydney) and the South Australian Museum (Adelaide); and to Dr. W. E. China of the British Museum (Natural History) for the opportunity to study material in his charge. The Senior Agricultural Officer, British Solomon Islands Protectorate, and his staff gave welcome assistance while collecting in the islands, and L. V. Waibuta and K. Nui assisted in collecting a great number of specimens during my work in the Solomon Islands. Finally, I wish to thank Dr. W. J. Hall, C.M.G., Director of the Commonwealth Institute of Entomology, and his staff, for assistance with the mounting and preparation of much of the material for study.

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FIG. 1. *Amblypelta cristobalensis*, sp.n., male. Scale in mm. alongside.

FIG. 2. *Amblypelta cocophaga cocophaga* China, male from Guadalcanal. Scale in mm. alongside.

INJURY TO CACAO BY *AMBLYPELTA* STÅL (HEMIPTERA, COREIDAE) WITH A SUMMARY OF FOOD-PLANTS OF SPECIES OF THIS GENUS.

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(Plates XIX–XXI.)

The recent increase in importance of cacao in New Guinea and the British Solomon Islands has resulted in increased knowledge of the insect pests of this crop in the south-west Pacific. As regards the Heteroptera, attention has mostly been concentrated on Miridae (*e.g.*, China & Carvalho, 1951; Miller, 1957; Dun, 1955). More recently, it has come to light that certain species of the Coreid genus *Amblypelta* can do considerable damage of an essentially similar nature. The probability that, as the cultivation of cacao becomes more intense, species of *Amblypelta* will become increasingly attentive to it as a food-plant, makes it advisable to place on record the facts so far as they are known.

Two species of the genus have so far been observed to feed on cacao: *Amblypelta cocophaga* China in the Solomon Islands (where it is also known as a serious coconut pest) and *A. theobromae* Brown (Brown, 1958, p. 524) in New Guinea. The damage done by these will now be described in turn.

Amblypelta cocophaga (in British Solomon Islands).

The first indication of damage by this species was noted at Auki on Malaita where the subspecies *A. cocophaga malaitensis* Brown (Brown, 1958, p. 529) occurs. Pods were found with circular, brown scars, which in severe cases and especially in pods at earlier stages of growth tended to coalesce and caused malformation and inhibited growth of the fruit (Pl. XX, fig. 2). These scars were essentially similar to those developing from feeding punctures of the Mirids *Helopeltis*, *Parabryocoropsis* and *Pseudodoniella*. A search revealed none of these Mirids, however, which have so far not been recorded from the Solomon Islands; but adults and larvae of *A. cocophaga* were found on the trees, and were occasionally seen feeding on the fruits, so that it seemed almost certain that this insect was the cause.

Later, *A. cocophaga malaitensis* was found on cacao at Saote, inland from Auki, in a small plantation which had recently come into bearing, and in which fruits with similar spotting had been found.

Apart from damage to the fruit, *A. cocophaga malaitensis* has also been noted attacking the terminal shoots of cacao on Malaita. This type of attack is found more typically in other plants, as will be seen later. In the case of cacao it results in a form of "die-back", although restricted to the extreme tip of the shoot so far as it has been observed up to the present. It threatens to become serious in some instances.

In order to confirm that *A. cocophaga* can produce scars on the pods of the type observed, experiments were carried out on a small cacao plot at Kukum on Guadalcanal; here the insect is represented by the subspecies *A. cocophaga cocophaga* China, which has, so far as is known, identical feeding habits. Trees were chosen on which there were a pair of fruits close together, and in a similar stage of growth. A muslin cage was suspended round one fruit of each pair, and three

or four examples of *Amblypelta* were placed in it. The bugs were seen to feed readily on the fruits, and sooner or later circular brown necrotic areas appeared round the feeding punctures; the other fruit of each pair, which was not enclosed, was not attacked, although there were a few individuals of *Amblypelta* on other food-plants not far away. Several such experiments were carried out, of which two will be described.

Experiment 1.

Two adjacent full-grown, but unripe, fruits 13 cm. long were chosen. One was caged on 8th June 1955, and four adults of *Amblypelta* were introduced. Small round circular feeding scars appeared within 24 hours, and by 16th June (8 days later), conspicuous brown feeding scars had appeared; the cage was then removed for purposes of examining and photographing the fruits (Pl. XIX, fig. 1). On 29th June (after a further 13 days) the scars had greatly expanded, and most of them had coalesced to form large necrotic lesions (Pl. XIX, fig. 2). By 5th August (37 days later and 58 days after the original introduction of the *Amblypelta*) the whole fruit had turned brown and had decidedly shrivelled; its diameter at the centre was 4·5 cm. compared with 6 cm. before the experiment began, while the other fruit was still about the same size (Pl. XIX, fig. 3). At this stage the two fruits were removed from the tree and cut in section; the pericarp of the caged fruit had shrunk to a thin, dry brown shell, and the seeds were shrivelled and brown (Pl. XIX, fig. 4); the uncaged fruit was still quite healthy.

Experiment 2.

Two younger, slender fruits were chosen, 11 cm. long, close to one another on the same branch. One was caged on 31st August 1956, and two adults and one larva of *Amblypelta* were introduced. On 3rd September (3 days later), circular brown feeding scars had appeared on the caged fruit; there were also a very few scars on the nearer side of the uncaged fruit due to the *Amblypelta* being able to reach it with their rostra through the muslin; this was prevented for the remainder of the experiment. The feeding scars gradually became more pronounced, and on 12th September (9 days later) the uncaged fruit had grown in length to 12 cm. while the caged one had shrunk to 10·5 cm. By 27th September (15 days later and 27 days after the experiment started) the uncaged fruit was still about 12 cm. long but the caged fruit had shrunk to 8·5 cm., and was shrivelled and brown (Pl. XX, fig. 1).

One would judge from this that although the adverse effects of feeding are more severe and rapid in a younger fruit than in a full-grown one (complete deterioration taking 27 days as compared with 58 days in these two particular experiments), damage can be disastrous even in the latter if feeding is sufficiently intense. Under the experimental conditions, feeding is likely to be more sustained on the individual fruits; in the natural state one would expect the severity of damage to be more widely graded according to the age of the fruit at the time of attack, such that light attack may have a disastrous effect on young fruits but a relatively unimportant one on full-grown fruits. This is borne out by observations at Auki, where it was found that younger fruits suffered more severely than older ones.

It is of interest that at Kukum, as mentioned above, the cacao was not attacked naturally although *Amblypelta* occurred within 100 yards and there were no species of ants present on the cacao trees which are known to protect the trees against *Amblypelta*. It may be that the Guadalcanal subspecies attacks cacao less readily than the Malaita subspecies; however, the experiments carried out show that it can attack cacao, and one should not underestimate the danger that it may turn its attention to it more, if and as this crop becomes cultivated more intensively.

Amblypelta theobromae **(in Papua, New Guinea).**

In December 1955, Dr. J. J. H. Szent-Ivany collected adults and larvae of a species of *Amblypelta* on cacao pods in Sangara Plantation, in the Popondetta district of Papua at an altitude of 1,000 ft. These proved to belong to an undescribed species, which has since been called *Amblypelta theobromae* (Brown, 1958, p. 524). The fact that immature stages were found as well as adults indicated that the insect was established and breeding on this food-plant.

In March 1956, an opportunity occurred for the author to visit Sangara Plantation in company with Dr. Szent-Ivany. *Amblypelta theobromae* was again found freely; the following is a list of the numbers of specimens captured on the pods of cacao:

	Males	Females	Larvae
20th March	4	3	2
21st March	6	7	–
22nd March	4	3	1
23rd March	4	3	8
Total	18	16	11

The presence of immature stages, and also the observed occurrence of several pairs mating, again suggests a well-established breeding of population.

During the same period, a few specimens (1 male, 3 females) were also found on rubber (*Hevea brasiliensis*) and a single female on cassava (*Manihot esculenta*); these two plants, however, were mainly attacked by the only other species of *Amblypelta* found in the district, namely *A. costalis* Van Duzee ssp. *szentivanyi* Brown (Brown, 1958, p. 531). The total numbers (including larvae) of the two species found on each food-plant were as follows:—

	A. theobromae	*A. costalis szentivanyi*
Cacao	45	–
Rubber	4	25
Cassava	1	9

The numbers are small, but it must be taken into account that *Amblypelta* is notorious for its ability to cause severe damage at very low population densities, and that the adults (especially of *A. theobromae*) are extremely active and difficult to catch. There is no doubt, however, that *A. theobromae* was strongly attached to cacao.

The extent of damage caused by the *Amblypelta* was very difficult to assess, because the Mirids, *Helopeltis* sp. and *Pseudodoniella* sp., were also abundant, and the damage to the fruits caused by these insects is of a similar nature to that caused by *Amblypelta*, and it would have been impossible to investigate the difference between them in the short time available.

In November 1956, at the invitation of Mr. J. H. Ardley, a visit was made to the Lae area in the Huon Gulf, Papua, where the cultivation of cacao had been increasing in recent years. *A. theobromae* was again found on the fruits of cacao in two plantations, Kunkamen and Leiwomba. In the former, ten specimens were captured, including three larvae and a pair mating, so that the insect was evidently established. In this plantation, a thorough search revealed no Mirids, nor any other insect likely to cause the heavy damage which was found, so that it is safe to attribute this to the *Amblypelta*. The damage took the form of round brown scars (Pl. XX, fig. 3) similar to those formed in the Kukum experiments. The scars differ from those caused by the Mirids, *Parabryocoropsis* and *Pseudodoniella*, in being larger and more evenly distributed over the surface of the fruit (those caused by the Mirids, especially the larvae, tend to be concentrated on the sheltered part of the fruit which is in contact with, or nearest to, the stem). In

cases of severe attack, the lesions had run together, to form large necrotic areas, and the fruit had become more or less distorted (Pl. XX, fig. 4). The scars may become infected with a fungus (probably *Gloeosporium*), in which case the central part of the scar becomes pushed up by the mycelium into a pustule, surrounded by an annular groove (Pl. XX, fig. 4, left- and right-hand fruits). The illustrations of damaged fruits leave no doubt that this insect is potentially a serious pest, which needs watching closely.

A study of a small area in which most of the trees were occupied by either of the ants, *Oecophylla smaragdina* (F.) or *Technomyrmex detorquens* (Wlk.), gave slight indication that the former gives some protection to cacao against attack by *A. theobromae* and by Mirids, in the same way that it protects coconuts against attack by *A. cocophaga*. The following figures were obtained:

Ant	No. trees	Percentage trees with one or more species of Hemiptera	Percentage trees with crop standards as shown		
			Good	Medium	Poor
Technomyrmex ..	26	65·4	0	7·5	92·5
Oecophylla	11	18·2	27·3	27·3	45·4

There is a tendency towards fewer Hemiptera and better crops on trees occupied by *Oecophylla* than on those occupied by *Technomyrmex*. One would not expect the correlation to be any more complete, because the distribution of ants was in a fluid state; there were a few trees, omitted from the figures, on which both ants occurred together, and others again with different species of ants.

As regards other species of *Amblypelta* attacking cacao, the only record is for *A. costalis szentivanyi* at Keravat in New Britain (observed by Mr. G. S. Dun); only one specimen has been captured; a few more were seen on cacao in the same locality and were probably of this same species since it is the only one so far recorded from New Britain. It does not appear to do any serious damage, and the fact that the same species is plentiful in the Popondetta district but does not attack cacao there, indicates that it is not likely to give any trouble unless it changes its habits.

Feeding Habits of *Amblypelta* spp. and Types of Damage caused.

There is now a good deal of information about feeding of economically important species of *Amblypelta* and about the nature of damage associated with them. The following summary is drawn mainly from personal observations, and from the published work of Brimblecombe (1948), Lever (1933), O'Connor (1950), Phillips (1940), Sloan (1946), Veitch & Simmonds (1929), Veitch & others (1951) and others.

Amblypelta may feed on three different parts of a plant, producing characteristic effects as described below.

(1). *Fruit.*

The most typical result is a sunken brown scar which develops round the feeding puncture made by the insertion of the rostrum. The scars are normally circular, as caused by *A. nitida* Stål on peaches (Anon., 1956, p. 10); by *A. lutescens lutescens* (Dist.) on bananas (well illustrated in Veitch & Simmonds, 1929, Pl. 31), and on pawpaw (Sloan, 1946); by *A. theobromae* and *A. cocophaga* on cacao (Pls. XIX & XX). The scars caused by *A. cocophaga* on coconut

are elongate rather than round, running down the long axis of the fruit (Phillips, 1940, Pl. XIII).

Sometimes no spotting of the fruit results from feeding, as in the case of *A. cocophaga* on grenadilla.

In the case of some crops the fruits fall prematurely shortly after feeding and the appearance of scars; thus *A. cocophaga* causes "immature nutfall" of coconuts, and *A. lutescens* has the same effect in the case of macadamia nut (Brimblecombe, 1948) and sometimes custard apple (Veitch & others, 1951); the age and size of the fruit is a factor which determines whether or not it will fall; a coconut is more likely to fall if attacked when very young than when it is older (Leach, 1950). In other cases (banana, pawpaw and cacao), the fruit does not normally fall as the result of attack.

Sometimes, in addition to discoloration, there is an exudation of gum from the scar (coconut, peach), or of latex (pawpaw). Thus immature nutfall of coconuts is sometimes called "gumming disease". The scars may become infected with fungi, as already described for cacao which may be infected by *Gloeosporium*; in this case the depression may then swell out again.

If the fruit survives an attack in the early stages of growth, subsequent growth following on the initial scar-formation may be irregular and uneven, resulting in distortion, as in cacao (Pl. XX, fig. 4), or in the formation of splits and cracks, as in bananas (Veitch & Simmonds, 1929, Pl. 32) and coconuts (Pl. XXI, fig. 4). Coconuts scarred in this way, but surviving, produce only about 65–96 per cent. of the copra they would have produced if undamaged, according to the extent of and age at which damage was done (calculated from figures obtained from Kukum and Tenaru on Guadalcanal, Solomon Islands).

(2). *Stem.*

Several species of *Amblypelta* are known to feed on the tender terminal shoots of trees and other plants; examples are *A. lutescens* on pawpaw, beans and macadamia nut, *A. cocophaga* on mango, *Ficus* spp., grenadilla and possibly cacao, *A. cocophaga malaitensis* on cacao (see p. 543), which may be economically important, *A. costalis szentivanyi* on rubber saplings (*Hevea brasiliensis*), and most species of the genus on cassava (*Manihot esculenta*).

The initial effect of feeding is usually the wilting of the shoot. *A. lutescens* may rapidly cause the death of young pawpaw plants. If the shoot survives, however, it may develop cankerous swellings and cracks; this is well illustrated by cassava when attacked by *A. cocophaga* (Pl. XXI, fig. 2), *A. costalis costalis*, *A. costalis szentivanyi*, *A. cristobalensis* Brown (Brown, 1958, p. 525) and doubtless other species. If the terminal bud is badly injured, lateral shoots may grow up to take its place, causing dichotomy or "bunching"; this occurs in pawpaw when attacked by *A. lutescens* (Sloan, 1946, Pls. 1 & 2).

In certain cases, however, little or no damage results from feeding on shoots; this was the case in New Guinea with *A. lutescens papuensis* Brown (Brown, 1958, p. 519) and *A. costalis szentivanyi* on rubber (*Hevea*). Mr. R. Leach, in an unpublished report to Levers Associated Enterprises Pty. Ltd., points out that *A. cocophaga*, when feeding from the tender shoots of the Euphorbiaceous shrub, *Macaranga tanarius*, produces no apparent external damage, but that this is deceptive, because the parenchyma cells are destroyed by the saliva and replaced by a resin which later forms a solid brown mass internally.

(3). *Petioles.*

Certain plants have soft petioles suitable for the feeding of *Amblypelta*. *A. lutescens* feeds on the petioles of pawpaw, causing cracks sometimes up to 4 in. long (Sloan, 1946). *A. cocophaga* sometimes feeds in the same way on petioles of cassava, and the result here is a pronounced downward drooping of the whole

leaf (well illustrated in Pl. XXI, fig. 2); cassava plants infested by *Amblypelta* can generally be recognised by this characteristic effect; the same effect is produced by *A. manihotis* (Blöte) (see Phillips, 1941).

A feature of *Amblypelta* damage which becomes strikingly obvious to anyone observing it in the field is that the effects are out of all proportion to (a) the physical damage done in feeding, and (b) the population density of the insect. *A. theobromae* produces on cacao the effects shown in Plate XX, figs. 3 and 4, at a population of considerably less than one insect in an active feeding stage (adult or larva) per tree. Similarly, *A. cocophaga* can produce severe coconut nut-fall at less than one active stage per palm. *A. l. lutescens* can cause stunting or distortion of pawpaw stems at one or two active stages per plant (Sloan, 1946), and one bug can cause collapse of a shoot of macadamia nut (Brimblecombe, 1948). Such severe effects are not normal for sucking insects, and can only be explained as resulting from injection of toxins into the plant tissues at the time of feeding.

Lists of known Food-plants of Species of *Amblypelta*.

Species of *Amblypelta* which have been studied in sufficient detail are known to be polyphagous; this applies only to *A. lutescens* and *A. cocophaga*, but although very few food-plants have been recorded for certain other species it is probable that they also will prove to exercise a wide choice of plants when more is known about them. A list of food-plants under botanical families, drawn up from personal observations and from the literature, will be given under each species. Where details have been recorded, the part or parts of the plant on which the insects feed will be indicated by "f" (fruit), "s" (stem) and "p" (petiole); where breeding on the plant is suggested, for instance by the presence of larvae, this will also be indicated (by the letter "*b*"). Native, uncultivated plants are indicated by an asterisk (*).

A. bilineata Stål.

Anacardiaceae.
Schinus terebinthifolius Raddi (f; *b*).

A. nitida Stål.

Rosaceae.
Prunus persica (L.) Batsch (peaches and nectarines) (f); *Prunus domestica* L. (plum) (f).

A. lutescens lutescens (Dist.).

Anacardiaceae.
Mangifera indica L. (mango) (f).

Annonaceae.
Annona squamosa L. (custard apple) (f).

Apocynaceae.
Plumeria sp. (frangipani) (f).

Bromeliaceae.
Ananas comosus (L.) Merr. (pineapple) (f).

Caricaceae.
Carica papaya L. (pawpaw) (f, s, p; *b*).

Compositae.
Xanthium strumarium L. (Noogoora burr).

EUPHORBIACEAE.
Manihot esculenta Crantz (cassava) (s; *b*).

LEGUMINOSAE.
Beans of various types (f); *Peltophorum pterocarpum* (DC.) Backer * (quoted as *P. ferrugineum* by Brimblecombe, 1948).

MALVACEAE.
Gossypium sp. (cotton).

MELIACEAE.
Melia dubia Cav.* (white cedar).

MORACEAE.
Ficus sp.* (rough-leaved fig).

MUSACEAE.
Musa paradisiaca L. (banana) (f).

NYCTAGINACEAE.
Calpidia brunoniana (Endl.) Heimerl * (quoted as *Pisonia brunoniana* by Brimblecombe, 1948).

PALMAE.
Cocos nucifera L. (coconut) (see Lepesme & others, 1947).

PASSIFLORACEAE.
Passiflora subpeltata Ortega (white passion flower); *P. edulis* Sims (passion fruit) (f); *P. quadrangularis* L. (grenadilla) (f); *P. suberosa* L. (corky passion flower).

PROTEACEAE.
Macadamia ternifolia F. Muell. (macadamia nut) (f, s; *b*).

RUTACEAE.
Citrus sp.

SAPINDACEAE.
Guioia semiglauca (F. Muell.) Radlk.*

Other recorded food-plants, which cannot be placed, are "Palay rubber vine" and "orange boxwood".*

A. lutescens papuensis Brown.

EUPHORBIACEAE.
Hevea brasiliensis Muell. Arg. (rubber) (s; *b*); *Manihot esculenta* Crantz (s).

LEGUMINOSAE.
Phaseolus mungo L.

MALVACEAE.
? *Urena lobata* L. (*b*).*

A. manihotis (Blöte).

Apart from *Manihot*, the following records are those given by Phillips (1941), who states that feeding was only recorded on *Albizia*; the other plants may only have been resting places.

EUPHORBIACEAE.
Manihot esculenta Crantz (s; *b*).

GRAMINEAE.
An unidentified grass.

LEGUMINOSAE.
Acacia villosa (Sw.) Willd.*; *Albizia falcata* (L.) Backer *; *A. lebbeck* (L.) Benth.*; *A. procera* (Roxb.) Benth.*; *A. chinensis* (Osb.) Merr.* (quoted as *A. stipulata* by Phillips, 1941); ? *Canavalia ensiformis* (L.) DC.*; *Dalbergia latifolia* Roxb.*; *Leucaena glauca* (L.) Benth.

STERCULIACEAE.
Melochia umbellata (Houtt.) Stapf *.

A. theobromae Brown.

EUPHORBIACEAE.
Hevea brasiliensis Muell. Arg. (s); *Manihot esculenta* Crantz.

STERCULIACEAE.
Theobroma cacao L. (f; *b*).

A. cocophaga cocophaga China and **A. cocophaga malaitensis** Brown.

These two subspecies of *A. cocophaga* are treated together since it is impossible in the case of some earlier records to state which is involved.

ANACARDIACEAE.
Mangifera indica L. (s, p).

BOMBACACEAE.
Ceiba pentandra (L.) Gaertn. ("kapok", probably refers to this sp.).

BURSERACEAE.
Canarium sp.* ("nali nut").

CARICACEAE.
Carica papaya L. (s, p; *b*).

CUCURBITACEAE.
Citrullus sp.? (Phillips' record (1940) for "melons" probably refers to some kind of water-melon).

EUPHORBIACEAE.
Codiaeum variegatum (L.) Bl.; *Euphorbia pulcherrima* Willd. (quoted as *Poinsettia pulcherimma* by Phillips, 1940); *Glochidion* sp.*; *Homalanthus populneus* (Giesel.) Pax * (? = *H. populifolius* quoted by Phillips, 1940) (s); *Jatropha curcas* L.; *Macaranga tanarius* (L.) Muell. Arg.* (s); *Manihot esculenta* Crantz (s, p; *b*).

GRAMINEAE.
Saccharum officinarum L. (sugar-cane).

LAURACEAE.
Actinodaphne solomonensis C. K. Allen.* (s).

LECYTHIDACEAE.
Barringtonia edulis Seem. (Lever, 1948).

LEGUMINOSAE.
"beans" (type unspecified); *Delonix regia* (Hook.) Raf. (quoted as *Poinciana regia* by Phillips, 1940) ("flamboyant") (f); *Vigna unguiculata* (L.) Walp. (cowpea).

MELASTOMACEAE.
Melastoma malabathricum L.* (f; *b*).

MELIACEAE.
Amoora sp.*; *Dysoxylum* sp.*

MORACEAE.

Ficus copiosa Steud.* (s; *b*); *Ficus septica* Burm. f.* (= *F. leucantotoma* as recorded by Phillips) (f, s); *Ficus* sp.* (Phillips records two other species of figs besides "*leucantotoma*", one of which may be *F. copiosa*).

PALMAE.

Cocos nucifera L. (f; *b*).

PANDANACEAE.

Sararanga sp. (f; *b*).

PASSIFLORACEAE.

Passiflora quadrangularis L. (grenadilla) (f. s; *b*).

POLYPODIACEAE.

Hypolepis tenuifolia (Forst. f.) Bernh.* (p; *b*).

RUTACEAE.

Citrus sp. (orange).

SAPINDACEAE.

Cupaniopsis sp.* (s).

SOLANACEAE.

Capsicum sp. (red chilli).

STERCULIACEAE.

Theobroma cacao L. (f, s; *b*).

TILIACEAE.

Triumfetta rhomboidea Jacq.* (quoted as *T. bartrami* by Phillips, 1940).

VITACEAE.

Leea indica (Burm. f.) Merr.* (quoted as *L. sambucina* by Phillips, 1940).

A. cocophaga has also been taken on an unidentified tree called by the natives "ayria", and by Phillips on "muscatels".

A. cristobalensis Brown.

EUPHORBIACEAE.

Manihot esculenta Crantz (s, p; *b*).

PALMAE.

Cocos nucifera L. (f; *b*). This is recorded by inference from the existence of immature nutfall on San Cristobal; although the insect was never actually taken on coconut, a nymph was found on the ground beneath a coconut palm.

A. costalis costalis Van Duzee.

CARICACEAE.

Carica papaya L. (p).

EUPHORBIACEAE.

Manihot esculenta Crantz (p; *b*).

PALMAE.

Cocos nucifera L. (f). By inference from the existence of immature nutfall on Bellona.

A. costalis rennellensis Brown.

CARICACEAE.

Carica papaya L. (p).

CONVOLVULACEAE.

Merrimia tuberosa (L.) Rendle * (s).

EUPHORBIACEAE.
Manihot esculenta Crantz (s).

PALMAE.
Cocos nucifera L. (f). By inference, from the existence of immature nutfall on Rennell.

RUBIACEAE.
Gen. nr. *Morinda* * (f; *b*). (Adults and larvae on red berries.)

A. costalis szentivanyi Brown.

EUPHORBIACEAE.
Hevea brasiliensis Muell. Arg. (s); *Manihot esculenta* Crantz (s, p; *b*).

STERCULIACEAE.
Theobroma cacao L.

A. gallegonis gallegonis Lever.

EUPHORBIACEAE.
Codiaeum variegatum (L.) Bl.; *Manihot esculenta* Crantz (s, p; *b*).

A. gallegonis bougainvillensis Brown.

CONVOLVULACEAE.
Ipomoea alba L.* (s; *b*); *I. batatas* (L.) Lam. (sweet potato).

EUPHORBIACEAE.
Manihot esculenta Crantz (s, p; *b*).

LEGUMINOSAE.
Pueraria phaseoloides (Roxb.) Benth.

PALMAE.
Cocos nucifera L. (f); fed in captivity; it has not yet been proved to do so in the natural state.

PIPERACEAE.
Piper sp.*

The only species for which no food-plants at all have been recorded so far are *A. brevicornis* Brown, *A. ardleyi* Brown and *A. blötei* Brown.

From the lists above it is clear that species of the genus have a wide range of possible food-plants; *A. lutescens* is recorded from 27 species in 18 families, and *A. cocophaga* from 35 species in 23 families. It is probable that when other species are better known they also will be found to feed on a comparable range of plants. The wide range of families represented under *A. cocophaga*, including, among others, Euphorbiaceae, Gramineae, Leguminosae, Palmae and even ferns, is very surprising.

The strong representation of the Euphorbiaceae is one of the striking features; for *A. cocophaga* it is represented by 8 species, or nearly 25 per cent. of the total.

Of the individual species which figure prominently, cassava is the most universal, 11 species and subspecies having been collected from it. One might regard it as an ancestral food-plant for the genus, were it not for the fact that it is an introduced plant from South America; it is, therefore, noteworthy that so many members of a purely Australasian genus have taken to it so readily. It has been the author's practice when looking for *Amblypelta* in a new locality always to look first on cassava. Any local species is usually to be found on it, especially on old stands mixed with other plants in overgrown cultivated areas (Pl. XXI, fig. 3).

Coconut is also a widely favoured food-plant; six species and subspecies are either known to feed on it, or else strongly suspected of doing so by inference from the existence of nutfall. Some appear to attack it more readily than others, and only *A. cocophaga* (Pl. XXI, fig. 1) has become a really serious pest on this crop.

It will be seen from the lists of known food-plants that the vast majority are cultivated or introduced. It is probable that there is a much greater range of indigenous food-plants, than is known at present. This is indicated by the discovery of *A. cocophaga* on certain trees in the forests of Guadalcanal (e.g., *Actinodaphne*, *Amoora*). On *Amoora* it was accidentally discovered (with the related Coreid, *Dasynus solomonensis* Brown (Brown, 1958, p. 536)) when a tree of this species was felled during clearing operations. It is probable that the forest canopy is the true home of the insect, in which case it would be difficult to ascertain its most favoured native food-plants.

What is known of the habits of the related genus *Pseudotheraptus*, in East Africa, suggests that this also may feed on a variety of plants (Way, 1953; Tait, 1954).

Summary.

Evidence is given, based on field observations and experiments, of damage to fruits of cacao by two species of *Amblypelta* (*A. theobromae* Brown in New Guinea and *A. cocophaga* China in the British Solomon Islands); the nature of the damage is described.

A summary is given of the feeding habits generally, and the effects on the plants attacked, of members of the genus *Amblypelta*.

Comprehensive lists of the known food-plants of each species of *Amblypelta* are given.

Acknowledgements.

I wish to thank members of the Agricultural Department in the British Solomon Islands (C. Mead, T. O'Leary, H. Roberts and J. Holsheimer) for obtaining specimens and information from various parts of the Islands; G. S. Dun, Dr. J. J. H. Szent-Ivany and J. H. Ardley for much information on species of *Amblypelta* in Papua and New Britain, and for assistance and cooperation during my visits to those territories; C. P. Hoyt, South Pacific Commission, and F. Cohic, Institut Français d'Océanie, for material and information from New Caledonia; and T. G. Campbell and C. E. Chadwick for information on Australian species. I am also indebted to the Keeper of Botany, British Museum (Natural History), and his staff for a number of identifications of plants, and for checking the names of plants referred to in this paper.

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FIG. 1. The right-hand pod has been caged with *Amblypelta* for 8 days, and the cage removed for photographing the pod. The scale is in cm.

FIG. 2. The same pods as in fig. 1, 13 days later. Feeding scars have coalesced to form larger necrotic areas.

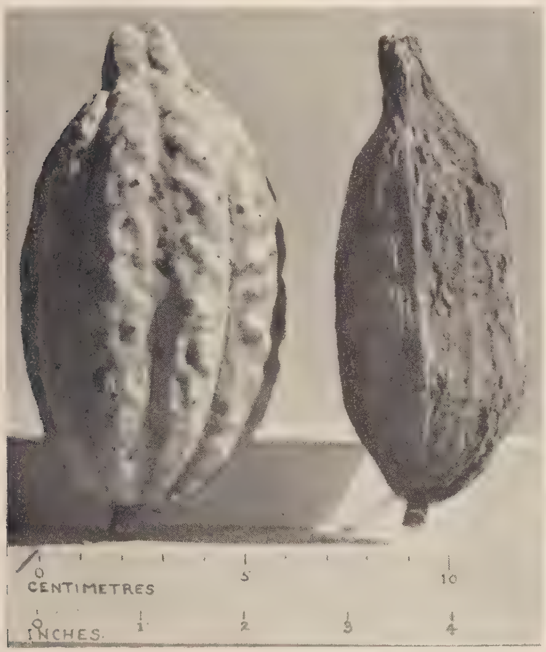

FIG. 3. The same pods as in fig. 2, removed from the tree 37 days later.

FIG. 4. The pods cut in section; that caged with *Amblypelta* is on the right.

CAGING OF *AMBLYPELTA COCOPHAGA* ON A CACAO POD (EXPERIMENT I).

FIG. 1. Last stage of Experiment 2 : the left-hand cacao pod has been caged with *Amblypelta cocophaga* for 27 days.

FIG. 2. Cacao pods damaged by *Amblypelta cocophaga malaitensis* at Auki, Malaita.

FIG. 3. Cacao pods damaged by *Amblypelta theobromae* at Kunkamen, Papua.

FIG. 4. Pods severely damaged and distorted by *A. theobromae* at Kunkamen, Papua.

CACAO PODS DAMAGED BY *AMBLYPELTA* SPP.

FIG. 1. Larva of *A. cocophaga cocophaga* on young coconut at Honiara, Guadalcanal.

FIG. 2. Damage to *Manihot esculenta* by *Amblypelta cocophaga cocophaga* at Honiara, Guadalcanal; note cankerous swellings on stem, and drooping petioles.

FIG. 3. An overgrown garden with old plants of *Manihot esculenta* at Boroni, San Cristobal; habitat of *Amblypelta cristobalensis.*

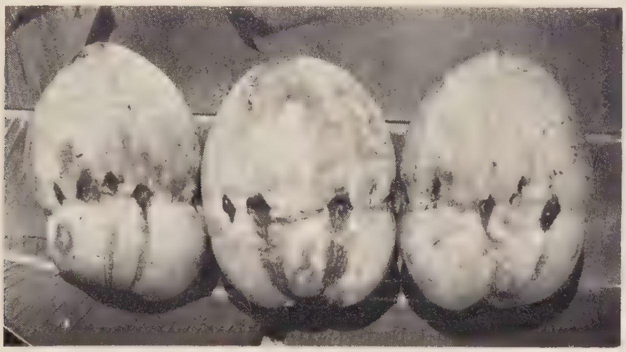

FIG. 4. Damage to coconuts by *Amblypelta* sp. at Sangara, near Popondetta, New Guinea.

HABITATS OF, AND DAMAGE BY, *AMBLYPELTA* SPP.

PROGRESS IN THE BIOLOGICAL TESTING OF SORGHUM MIDGE (*CONTARINIA* SPP.).

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Sorghum Midge is a pest of some importance wherever sorghums are grown and may be considered to comprise three morphologically similar species of the genus *Contarinia*. *C. sorghicola* (Coq.) was originally described from Texas, U.S.A., and what is by morphological criteria apparently the same species has since been reported from many parts of the world including the West Indies, Venezuela, Hawaii, Australia (Queensland), Indonesia and East and West Africa. The two very similar species, *C. caudata* Felt and *C. andropoginis* Felt, were described from India. In addition, two other Bifila species and at least one species belonging to the Lasiopterariae have been reared from sorghum heads and may attain the status of pests, but these are not considered here; further details are given by Barnes (1956).

The desirability of biological experimentation in order to establish whether Sorghum Midge consists of several species that have arisen independently in the various countries or is one species that has been transported from country to country with the sorghums was stressed at the Sixth Commonwealth Entomological Conference in July 1954 (Barnes, 1954*a*, *b*). The successful emergence of *C. sorghicola* and its parasite *Eupelmus popa* Gir. from material from the Gambia at Rothamsted Experimental Station was also reported.

The object of this paper is to record what further progress has been made.

Thanks to the co-operation respectively of Dr. E. S. Narayanan, Head of the Division of Entomology at the Indian Agricultural Research Institute, New Delhi, at the time, and of Mr. J. Bowden, while Senior Entomologist, Department of Agriculture, Ghana, I have been able to import midge-infested heads of sorghum from Narasipur and Chitaldrong, Mysore State, India, and from Nyankpala and Tamale, Northern Territories, Ghana, under licences issued by the Ministry of Agriculture, Fisheries and Food. From these samples, midges and parasites have emerged under laboratory conditions in the new West Building at Rothamsted Experimental Station; there appeared to be no morphological grounds on which the midges could be separated from the *C. sorghicola* of Texas. All the material, either in emergence or in "detector" cages, was kept moist from the date of receipt (see below) until the summer of 1956 when it was allowed to dry out. It was re-wetted early the following December and kept moist until April 1957 when all the material, except the portion of the sample from Tamale that had been placed in a detector cage, was allowed to dry out. Finally, all the material was steam sterilised in September 1957.

Emergence of Indian Midges and Parasites.

The Indian samples had been collected in September and October 1955 and were received the following January. It will be seen from Table I that, whereas most of the parasites emerged during the first period that the samples were kept moist, the emergence of the midges was confined to the second period. In all, 13 males and 95 females of the midge and 237 parasites emerged.

Some of the parasites were identified by G. J. Kerrich as *Tetrastichus* sp., group of *flavovarius*, auct. He noted that "they resemble the species reared by

Q. A. Geering in Tanganyika in 1953, notably in the prominent bright yellow coloration unusual in *Tetrastichus*. These (the African and Asiatic) are probably closely related, but clearly not actually the same species". Others were identified by R. D. Eady as *Eupelmus popa*.

TABLE I.

Emergence of midges and parasites from material from India.

Locality	Periods of emergence	Midges Males	Midges Females	Parasites
Narasipur	Jan.–Aug. 1956	0	0	214
,,	Feb.–Apr. 1957	3	13	6
Chitaldrong	June–July 1956	0	0	2
,, ...	Feb.–Apr. 1957	10	82	15

Emergence of West African Midges and Parasites.

The West African samples had been collected in November and December 1955 and were received the following February. A considerable number of midges had emerged during transit. It will be seen from Table II that, as in the case of the Indian material, most of the parasites emerged during the first period that the material was kept moist and the emergence of the midges was again confined to the second period. The portion of the Tamale sample that had been placed in a detector cage was kept moist until it was finally destroyed by sterilisation. The majority of the midges emerged in this particular sample during July and August 1957.

TABLE II.

Emergence of midges and parasites from material from West Africa.

Locality	Periods of emergence	Midges Males	Midges Females	Parasites
Nyankpala (native farm)	Apr.–May 1957	0	0	12
,, ,, ,,	Mar.–Apr. 1957	3	14	0
Nyankpala (C.A.S.) ..	April 1956	0	0	5
,, ,, ..	Mar.–Apr. 1957	3	9	1
Tamale	Apr.–May 1956	0	0	2
,, ...	Mar.–Aug. 1957	6	24	1

All the parasites, except one, were identified as *Tetrastichus* sp., group of *flavovarius*, auct., by G. J. Kerrich who noted that these all represent a species closely resembling in structure that bred by Q. A. Geering from Tanganyika material, although it must be regarded provisionally as different, and very distinct from the species bred by Q. A. Geering in Uganda (Geering, 1953). The

remaining individual with determined by R. D. Eady as *Eupelmus popa*. It was reared from the material from the Central Agricultural Station, Nyankpala, in 1957.

Inter-mating of Indian and African Midges.

There were few days on which newly emerged midges from both India and West Africa were available for inter-mating experiments, but on five days experiments were made. In the first, an Indian male was placed in a glass tube with an African female. The male was greatly excited, the female waved her fully extended ovipositor, but no mating took place. When the male was placed in a glass tube with an Indian female, both midges exhibited the same behaviour as before, but again no mating occurred. In the second experiment, an African male was placed first in a glass tube and then in a small muslin cage with an Indian female. Typical sexual excitement was exhibited by both midges, but no mating took place. An Indian male was substituted for the African male. Again both midges showed the same sex behaviour, but once again no mating took place. In the third experiment, a male from Nyankpala (Africa) mated in rapid succession with two out of three females from Chitaldrong (India) in a small muslin cage, but after 30 minutes had not mated with the third female. This male and three females, as well as other specimens of both the Ghana and the Mysore midges are in the Barnes collection. In the fourth experiment, two males from Chitaldrong became vastly excited in the presence of a female from Nyankpala, but neither actually mated. In the last experiment, a male from Narasipur and a female from Tamale were confined together. Typical sexual excitement was exhibited by both midges but once more no mating took place.

While these experiments were not entirely satisfactory owing to the laboratory atmosphere in which they were carried out and the fact that on most occasions the males apparently became too excited to mate and soon became exhausted by their wild flutterings within the tube and muslin cages, it seems apparent that, given suitable conditions, the midges from India and West Africa would have inter-mated. In fact, on two occasions actual mating was observed as stated above.

Unfortunately, no sorghum plants at the suitable stage of growth for oviposition were available at the time, so no evidence has yet been obtained as to the fertility of such inter-matings.

Summary.

Successful emergence of examples of *Contarinia* sp. and associated parasites has been obtained at Rothamsted Experimental Station from midge-infested heads of sorghum received from India (Mysore State) and West Africa (Ghana).

Since typical pre-mating behaviour was observed on all of the few occasions when newly emerged males and females from the two continents were confined together, and actual mating was obtained between a male from Ghana and two females from Mysore in rapid succession, it is concluded that inter-mating will take place under suitable environmental conditions, although in the present series of experiments such conditions were rarely present.

It has not yet been possible to test the fertility of such inter-matings or to prove biologically that the species of *Contarinia* concerned is the *C. sorghicola* (Coq.) of Texas, although on morphological grounds there are apparently no reasons for their separation.

Two species of parasites, a *Tetrastichus* sp. (group of *flavovarius*, auct.) and *Eupelmus popa* Gir., were reared from the Indian material, and another species of *Tetrastichus* (group of *flavovarius*, auct.) and *E. popa* were reared from the West African material.

Acknowledgements.

I am indebted to the Commonwealth Institute of Entomology, and in particular to Messrs. G. J. Kerrich and R. D. Eady, for the identification of the parasites that emerged.

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STUDIES ON THE COCONUT PEST, *PSEUDOTHERAPTUS WAYI* BROWN (COREIDAE), IN ZANZIBAR.

I.—A METHOD OF ASSESSING THE DAMAGE CAUSED BY THE INSECT.

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(Plates XXII & XXIII.)

The Coreid, *Pseudotheraptus wayi* Brown, formerly known as *Theraptus* sp., causes very heavy damage to the fruits of the coconut palm, *Cocos nucifera* (Way, 1951, 1953*a*, *b*; Vanderplank, 1953) and of certain other plants (Tait, 1954). In its behaviour and in the nature of the damage it causes, it is very similar to *Amblypelta cocophaga* China (Lever, 1935; Phillips, 1940; Leach, 1949; O'Connor, 1950).

P. wayi lives and feeds in the crowns of coconut palms and this makes its collection difficult. The adults are winged and fly off when disturbed, and the young are extremely agile and readily hide in the numerous crevices of the inflorescences and spadices. Attempts to collect the living insects are thus slow, laborious and frequently unreliable, and it was necessary to develop a rapid and reliable method of assessing the damage caused by this insect which could be used to estimate the effectiveness of control methods that were being tested.

Early Methods tested.

P. wayi is difficult to find, on account of its low population density. The first method tried was hand-collection by the scientific staff studying the pest, operating with various forms of ladder (Pl. XXII, fig. 1) and by local climbers directly scaling the trunks. With the former method, work is very slow on account of the moving of the ladders (about one hour per palm being required), and with the latter, although it is rather quicker, the work tends to be of a variable quality in the absence of direct supervision.

Way attempted to collect *P. wayi* by employing a climber to apply a pyrethrum-based spray to the crowns of selected palms, with 50-sq. yd. sheets spread out at the bases. This method has the disadvantage that the slightest breeze causes the falling insects to be carried away and lost; as all the insects are not affected immediately, a long period of still air is essential. The writer modified this method by applying a knockdown spray with a "Micron" machine (Vanderplank, 1954), again with erratic results. Sticky papers, patches and bands were all tried in various parts of the crowns but, except for those placed on the trunks 1–3 ft. below the lowest leaves, no individuals of *P. wayi* were caught by this method.

Light-traps in the crowns were unsuccessful, and laboratory tests failed to show any attractive or other effects of light on any of the life-stages, though in nature the insects have a certain preference for dark green, brown and orange backgrounds.

Marking and recapture methods such as are used with tsetse flies cannot be applied to adults of *P. wayi*, owing to their rarity and mobility, which precludes

their being followed from palm to palm with a net. Marking of nymphs by normal means is largely wasted labour, as the marks are shed with the skin at ecdysis. Other methods were therefore examined.

Radioactive Marking Techniques.

Nymphs were reared on coconut inflorescences placed in distilled water containing ^{32}P or ^{35}S at the rate of 2 millicuries per pint. The ^{32}P was in the form of carrier-free orthophosphate in dilute hydrochloric acid (pH 3–5) and original activity of 8·83 mc./ml. The ^{35}S was in the form of a sulphate containing a little sodium chloride (pH 1–2) with the carrier sulphate not exceeding 100 μg./ml. and an activity of 5 mc./ml.

The inflorescences became radioactive within 24 hours and sections which were autoradiographed showed that, whereas the phosphorus was distributed chiefly in the meristematic tissues, on some of which *P. wayi* feeds, the distribution of the sulphur was more uniform. Nymphs reared on these inflorescences became strongly radioactive.

Radioactivity was detected by a portable radioactive ore detector (P.R.O.D.) made by E. K. Cole, Ltd. This consists of a battery-operated amplifier with Geiger-Muller tube and headphones. The background radiation recorded with the instrument is about 100 counts per minute, but adults of *P. wayi* reared from nymphs fed on radioactive inflorescences gave rates of over 600 counts. The half-life of ^{32}P is short for release-recapture studies and the longer-lived ^{35}S is more suitable in this respect.

Several hundred radioactive adults were released in a relatively isolated plantation 800 yd. long by 50–100 yd. wide, with palms spaced roughly 10 × 10 yd. apart. Searches were then carried out by a climber who scaled each palm and assayed the crown with the P.R.O.D. whilst the writer stood beneath wearing the headphones. Radioactive adults were detectable as far as 4 ft. from the Geiger-Muller tube, but they generally flew away when approached closer than one foot.

Although some data on the movement of individuals were obtained by this method, it proved too clumsy for use as a basis for determining the size of a population.

Notes on the Growth of Coconut Palms in Zanzibar.

Some explanation of the nature of the growth and of the flowering and fruiting habits of the coconut palm is necessary in order to understand the method eventually adopted for estimating populations of *P. wayi* and the damage caused by them. No data were available in regard to these subjects under local conditions in Zanzibar, and it was necessary to carry out a considerable number of observations.

There are a number of different types of coconut palm, the important differences between them being in the size of the nut, particularly in relation to copra content, and the number of nuts borne. Only one variety, the King coconut, is quite distinct from the others. It has a small orange-coloured nut with a sweet juice and is grown for drinking; its "meat" is unsuitable for copra. This variety is found dispersed throughout the plantations, but it is omitted from the following observations on the copra-producing varieties.

The coconut palm usually commences to bear fruit when it is six to eight years old and the height of the trunk from the ground level to the base of the crown is then about 8–10 ft. At the centre of the crown is a spike of developing leaves and inflorescences surrounding the single growing point. The leaf arrangement is what is known as two-fifths phyllotaxis. Each new leaf is given off at an angle of about 142° round the stem, thus the sixth leaf is at 142° × 5 = 710°.

or nearly twice round the stem (Sampson, 1923). The order in which both leaves and inflorescences open may constitute either a clockwise or anti-clockwise spiral rotation. In healthy, vigorous palms, each leaf is from 12–16 ft. long and 5–7 ft. across at its maximum breadth, and there may be from 30 to 45 leaves. The old leaves and spadices fall off in rotation. The trunk does not elongate or increase further in girth, all new growth taking place at the tip. In the first three years, only the bole of the palm is formed, and in the following four or five years the palm grows 8–10 ft., or an average of 2 ft. per year. A fifteen-year-old palm stands about 20 ft. high (all height measurements are from the ground to the base of the crown; the top of the crown will be 10–18 ft. higher). A thirty-year-old palm is about 30 ft., and one fifty years old about 45 ft. high. These figures are averaged from 50 samples in each stage of growth. There are many factors affecting the growth of a palm, particularly soil drainage. I have seen some palms on Mafia Island, known to be over 50 years old and growing in a seasonal swamp, which are only 10 ft. high and their leaves only 4 ft. long, but these are extreme cases.

Records have been kept over five years of the frequency with which successive inflorescences open, and of the subsequent development of the flowers and nuts. Records from some 50 palms show that the number of inflorescences opening per palm per annum ranged from 12, on large-nut palms, to 18, on small-nut ones. Each inflorescence has several hundred male flowers on the extremities of the spicules, and from 10 to about 75 female flowers (Pl. XXII, figs. 2 & 3), provided that it is not being damaged by *P. wayi* or the weevil, *Diocalandra frumenti* (F.). These insects cause a marked change in the growth of the palm, which is discussed later. The observations considered were made on palms protected by very strong colonies of the red tree-ant, *Oecophylla longinoda* (Latr.), and more recently by regular applications of insecticide. Five to seven days after the inflorescence has emerged from its tough protective spathe, the male flowers start to open, commencing at the extremity of each spicule. Each remains open 2–3 days and then falls off. This process takes 10–15 days, by which time all the male flowers have abscissed. The above statements are in agreement with Sampson (1923) and Leach (1949), but not, entirely, with Way (1953*a*), who stated that the male flowers open within 2–4 weeks, just before the female, and that pollination usually takes place after about five weeks.

The female flowers open almost simultaneously, and from 7 to 10 days after all the male flowers have fallen off (Pl. XXII, fig. 3). This has been observed consistently in all the numerous palms observed over periods of up to four years.

Although, as Way (1953*a*) states, the number of flowers varies from palm to palm according to their age and variety, I have not found, in palms free from insect damage, any seasonal variation such as he claims, but his observations may have been affected by the presence of *P. wayi*. In the absence of *P. wayi* and *D. frumenti*, the female flower remains open for two days, after which the stigma turns red and then dries up. A week to 14 days after fertilisation, from 20 per cent. (in varieties with large nuts and few flowers) to 80 per cent. (in varieties with small nuts and numerous flowers) of the nutlets absciss. Many of these lodge in the leaf axils, and only a small proportion falls to the ground. When such nutlet absciss they are fresh and, if the calyx is removed, the sub-calyx tissues show up white and unblemished. These fallen nutlets turn brown within a week and eventually rot. When no insect or fungal damage takes place, no further nutfall occurs, and the young nuts develop rapidly. Prior to fertilisation of the flowers, which takes place 3–4½ weeks after the inflorescence has opened, no flower-buds or flowers are shed from palms protected from *P. wayi* and *D. frumenti*. The above is at variance with Way (1953*a*) who states that the "natural" fall of a varying proportion of young nuts occurs when they are about 5–10 weeks old.

The young inflorescences remain in a near-vertical position, but as the nuts develop the bunch bends downwards due to its increased weight and to the development of further leaves and inflorescences above it. The nuts elongate from the meristem, which is basal and protected by the calyx, and they are three-quarters grown after six months. The growth rate has been studied by making a mark on the nut, along the edge of the calyx, at weekly or monthly intervals (Pl. XXIII, fig. 2), in the same way as was described and well illustrated by O'Connor (1950) for coconuts in the British Solomon Islands. This paper includes a statement by R. Leach that the daily elongation of a nut averages about 1·5 mm. In Zanzibar, the average length, measured from the edge of the calyx to the tip of the nutlet, is 0·4 cm. one month after the opening of the spadix. This is the stage at which the flower opens and is fertilised. At this stage the fruiting body is about 3–7 cm. across, depending on the variety of palm.

The average elongation in successive months is as follows:

Month of life	Growth in length (cm.)	Monthly growth as percentage of final length
1	0·4	1·5
2	5·1	19·6
3	4·3	16·5
4	4·1	15·8
5	3·8	14·6
6	3·5	13·5
7	2·1	
8	1·1	
9	0·8	18·5
10	0·4	
11	0·4	
Total	26·0	100·0

When six months old, a nut is approximately 75 per cent. of its final weight and volume. These figures compare with the statement by Way (1953*a*) that the nut is full sized after 5–6 months, but not mature until after 11–13 months.

Each leaf should have an inflorescence in its axil, but this is not so in the majority of palms in Zanzibar, where the number of inflorescences borne by a healthy palm varies with the type of palm, climatic conditions, soil and insect damage. Omitting insect-damaged palms and taking an average from various types of soils and palms over five years, I have found the interval between the opening of successive inflorescences to be 22½ days, so that just over 16 inflorescences are produced each year. The average number of inflorescences and bunches of nuts counted on 400 palms, undamaged by insects, taken at random over various Government plantations, was likewise 16 per palm. It has been mentioned earlier in this paper that this number varies from 12 in large-nut palms to 18 in small-nut ones.

Effect of *P. wayi* on the Growth of Nuts.

When an adult of *P. wayi*, or a nymph in any but the first instar, feeds upon a coconut-palm fruiting body (that is, a flower-bud, flower or nut), a necrotic lesion develops in the tissues at the site of the puncture. Providing the fruiting body is under three months old (timed from the opening of the spadix), it is normally shed within four to seven days, but if the puncture is not a severe one, abscission may be delayed for as long as 14 days, unless secondarily infested with the larvae of *D. frumenti*. Very similar damage is caused in the Solomon

Islands by the related Coreid, *Amblypelta cocophaga* (Phillips, 1940; O'Connor, 1950).

The Kiswahili word for the developing fruiting body during the first three months after the opening of the spadix is *kidaka* (plural, *vidaka*) and it is used here to denote this stage in the development. The succeeding stage is termed *kitale* (plural, *vitale*), and there are other terms for the later stages in development. Examples of vidaka and vitale are illustrated in Pl. XXIII, fig. 1.

In areas heavily infested with *P. wayi*, the palms yield very few mature nuts; the average yield is sometimes as low as 4 nuts per palm per annum. In such areas, the palms appear more vigorous than in less heavily infested ones, and have more leaves per palm, more flower-buds and, consequently, flowers per inflorescence, and more inflorescences per annum. Several such areas received insecticidal treatment over a period of 18–24 months, and in one 30-acre plot the yield per palm per annum was increased from an average of 4–6 nuts to 50 nuts; similarly, in two 10-acre plots, the yields were raised from 8–12 nuts to 33 and 50 nuts. In none of the experiments was full control of *P. wayi* obtained, but the damage caused by it was reduced very considerably. In these areas the average number of flowers per inflorescence fell from 200 to 75 and from 17–18 inflorescences per year to 15–16.

In areas entirely free of *P. wayi*, such as Chumbe Island off Zanzibar and Bwejuu Island near Mafia Island, the only fallen fruiting bodies that can be found on the ground are nutlets from recent flowers. In a 100-acre plot treated at regular intervals with insecticide, where damage by *P. wayi* and *D. frumenti* has been reduced to negligible proportions, examination of over 20,000 fallen fruiting bodies showed that over 99 per cent. had fallen about a week after flowering. On the other hand, in areas where damage by *P. wayi* is prevalent, a high but varying proportion of the fallen material consists of flower-buds, flowers and nuts in the later stages of development, as distinct from recently-formed nuts. Some samples have shown as high as 70 per cent. of pre-fertilisation stages. Not all of these fruiting bodies show signs of insect damage, but it is usual that at least half of them show one or more lesions attributable to *P. wayi*. As the nut develops, its abscission becomes increasingly unlikely, but each puncture forms a lesion that results in permanent scarring and distortion of the nut. *P. wayi* feeds only through the calyx and its stylets penetrate the meristematic tissues, which are broken down by the insect's saliva. A cavity is formed which is usually filled with a gum-like substance secreted by the plant, and where the lesion is large, this gum oozes out and hardens on the outside of the nut. Such lesions are often invaded by various yeasts or other fungi and serve as breeding sites for *D. frumenti*. Vidaka or nuts infested with larvae of *D. frumenti* neither fall off nor grow, but remain in an apparently healthy state for several months. Even after the vidaka have eventually dried up, they remain attached to the spadix until this falls from the palm.

The effect of *P. wayi* on neighbouring undamaged flowers has been investigated by covering each of ten newly opened spadices with fine cotton netting. Various stages of *P. wayi* were introduced into half of these, and the remainder were kept as controls. In the controls, no flower-buds or pre-fertilised flowers were shed, but where *P. wayi* was introduced, the punctured flower-buds and pre-fertilised flowers were shed, and also a number of others that were not punctured. The extent and implications of this phenomenon are as yet not fully understood.

Considerations affecting the Choice of a Method of Estimating the Numbers of *P. wayi* or the Damage it Causes.

The yield is the ultimate test of any control method, but while the many possible methods of control are being investigated, a quick, practical method of

assessing results is essential. One method that has been used is to search for nymphs of *P. wayi* in the crowns of the palms. This has been carried out by six to nine trained climbers during three years, and the results of searching some 40,000 palms have been recorded. The slowness and expense of this method, although not so important in a research project, would prohibit it as a general method of assessing damage by *P. wayi* throughout East Africa. The main objections to the method are that in practice it has given erratic results when used to assess the effectiveness of control measures and that, because the adults fly away when approached, it gives no indication of the adult population of *P. wayi*, which may be either smaller or greater than the population of nymphs.

Since the necrotic lesion caused by *P. wayi* (Pl. XXIII, fig. 1) is quite distinctive, no similar damage being caused in Zanzibar by any other insect, and since all punctured vidaka (except for those attacked by *D. frumenti*) are shed within a few days and rot within a week of falling, the numbers of *P. wayi* or at least the degree of damage caused by them could be assessed by a count of the damaged vidaka. Since neither all the fallen vidaka, nor a constant proportion of them, could be collected, it was necessary to discover some means by which comparable counts could be made.

Observations by the author and by other workers (Way, 1953*a*) have shown that in certain conditions *P. wayi* can destroy 98 per cent. of the coconut crop. In such areas, when as many as possible of the fallen vidaka and immature nuts are collected and examined, some 70–90 per cent. are found to be damaged by *P. wayi*. The fallen material includes a proportion of unopened flower-buds, flowers before and after fertilisation, and older nuts. Since the growth rate of the nut is reasonably constant, the approximate age of any of these fallen fruiting bodies can be estimated. This has already been pointed out by O'Connor (1950) as true for the Solomon Islands. Practically all the fallen fruiting bodies that are older than the stage at which natural fall occurs (shortly after fertilisation) can be seen to have been damaged by *P. wayi*. Some may show damage by the Pyralid borer, *Lamoria* sp., or a pink ring in the meristematic tissues, suggesting some fungal infection, but these are infrequent compared with those damaged by *P. wayi*.

Theoretically, the best method of comparing different areas would be to collect all the fallen fruiting bodies in each of them and assess the severity of the infestation by the total number showing damage by *P. wayi*. This is impracticable, however, because quite a large number of those falling become lodged in the axils of the leaves and rot. Those that fall to the ground are difficult to find in some areas because of the thick growth of herbs and shrubs, and even where the ground is clear of vegetation, it would be extremely difficult to collect all the fallen material and would require much labour and supervision.

If any control measure gave 100 per cent. kill of *P. wayi*, then none of the fallen material would show any recent damage by the insect, although older nuts would show scars from earlier attacks. This was found to be the case after a double application * of insecticide had been applied from the air to over 600 acres of coconut plantation in October 1952. Several thousand fallen fruiting bodies were examined following the sprayings. Prior to spraying, examination of several hundred fallen fruiting bodies collected at random in the proposed experimental areas showed that over 90 per cent. had been damaged by *P. wayi*. Seven days after the first application, 61 per cent. of several hundred examined showed damage by *P. wayi*. One month later, out of nearly a thousand collected at random, none showed any such damage. Ten weeks later, 1·5 per cent. of those collected showed damage and thereafter the proportion increased until, six months later, 99 per cent. showed damage by *P. wayi*.

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* Two applications, at an interval of 9–10 days, are usual, the object of the second being to kill any immature stages that have hatched since the first.

The actual number of necrotic lesions on a kidaka varies from one to over 32, and often more on an older nut. Weekly records were kept during 1953 and onwards from several plantations used as controls and from others used for experimental applications of insecticides. Three methods of collecting the fallen vidaka were tried: (1) at least 100 were gathered at random, at the rate, if possible, of not less than 10 per acre, (2) all the fallen vidaka were gathered from below at least 100 palms taken at random, or (3) from rows of palms selected at random. The numbers with and without damage by *P. wayi* were recorded. The results from these three methods of collecting the fallen vidaka did not differ significantly, but more labour was required to collect the vidaka by the two latter methods.

In unsprayed plantations, the proportion of vidaka damaged by *P. wayi* shows an irregular fluctuation, and some seasonal variation, but remains broadly constant within the limits of experimental error. Results obtained from two different areas over a fifteen-month period are given in fig. 1. They are expressed in terms of the vidaka damage rate, which is defined below.

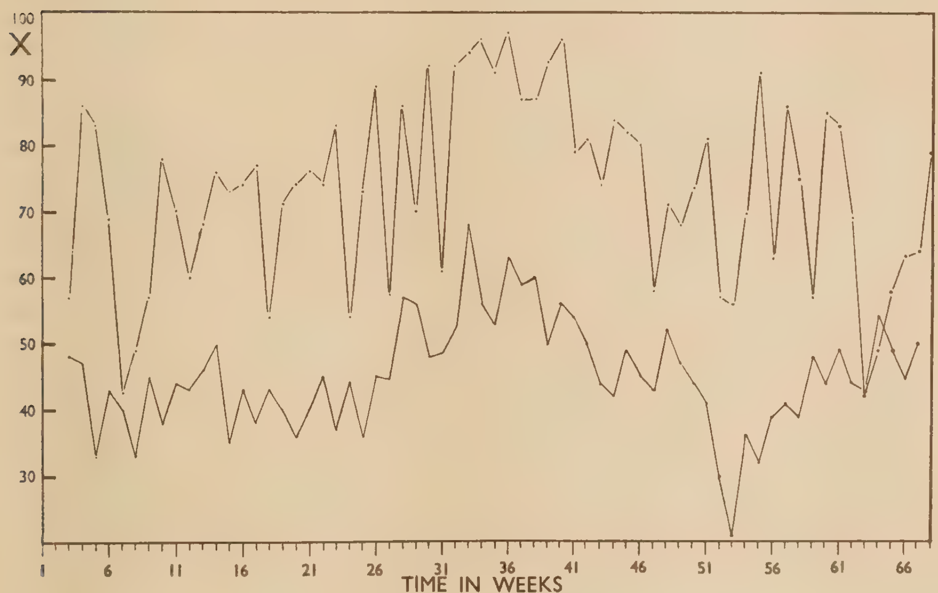


Fig. 1.—Weekly vidaka damage rate (X) from two untreated plots of coconut palms. Above: Mazizini control plot (2 acres, 100 palms). Below: Kizimbani control plot (100 acres, 4,250 palms). Week 1: week ending 7.iii.55.

It was found that, in the laboratory, during the warmer part of the year, adults and nymphs of *P. wayi* each made, on an average, five punctures a day, whereas in the cooler season the daily average was only three. Moreover, if continually disturbed, both adults and nymphs made many more punctures, depending on the amount of disturbance. The severity of the effects following a puncture is, furthermore, related to the stage of development of the individual that has inflicted it. The number of damaged vidaka found was greater in the warm than in the cool season, but not in the proportions of 5:3, as might be

expected from the laboratory results; the increase amounted to up to 20 per cent. However, the average number of punctures per damaged nut was found to vary considerably from locality to locality, and particularly from one ecological complex to another.

Although subject to several objections, and liable to considerable theoretical variation, it has been found during six years that the proportion of vidaka that show damage by *P. wayi* gives a good indication of crop loss, and can be used as a reliable guide to the effectiveness of any control measure being tested.

The measurement employed, termed the vidaka damage rate (or V.D.R.), is defined as the number of vidaka showing damage by *P. wayi*, expressed as a percentage of the total number of fallen vidaka collected. The vidaka must be freshly fallen ones that have not started to turn brown, and an adequate random sample must be collected.

Although the method is undoubtedly inaccurate for assessing heavy damage, it becomes more accurate as the population of *P. wayi* is reduced, and constitutes a cheap and effective routine which, with trained personnel, could be further refined. One labourer can usually collect well over 100 vidaka from a 10-acre plot during a morning's work. To sample a 100-acre plot we aim to collect at least 1,000 vidaka each week; to do this, three labourers are employed three days a week, but during dry weather it is necessary to double the number of labourers to obtain this number.

Discussion of the Vidaka Damage Rate.

It has already been pointed out that a high percentage of the nutlets are shed shortly after flowering, even when *P. wayi* is not present, but that where the insect occurs, flower-buds, flowers and older nutlets are also shed, following puncturing by the insect. It is possible to recognise the immediate post-fertilisation stage by careful examination of the stigma, which will have turned brown and dried up, and by the size of the nutlet. A less variable figure for the V.D.R. should be obtained if it were based solely on this particular stage, that is, that reached within a few days of fertilisation, when the stigma is still visible and *before* natural nutfall occurs. This method has been investigated and found to reduce the standard error, but it has not been generally used, since a trained person would be necessary to examine each nutlet individually. A typical example for the week ending 18.v.57 was as follows. From a 100-acre area that was not treated in any way, 1,611 fallen vidaka were examined, of which 714 (44·3 per cent.) showed damage by *P. wayi*. Of the total, 585 (or 36·3 per cent.) were in pre-fertilisation stages, and of these, 269 (or 46·0 per cent. of them) had been damaged by *P. wayi*. The number of vidaka that could be considered to be nutlets in the stage at which normal nutfall occurs was 1,016, and of these 435 (or 42·8 per cent. of them) showed damage by *P. wayi*. The two estimates of percentage damage do not differ from each other significantly by the χ^2 test. The ten remaining fruiting bodies that had been gathered as vidaka were, in fact, older nutlets, and all had been damaged by *P. wayi*. As already stated, older fallen nutlets invariably show damage by *P. wayi* or other insects, or by fungi, and for this reason are not included in the counts. No fallen fruiting body with an overall length exceeding three inches is included in the examination; this size is reached about 2½ months after the opening of the spadix. In a 100-acre experimentally sprayed area during the same week, 1,499 fallen vidaka were collected, of which 134 (8·95 per cent.) showed damage by *P. wayi*. Only six of the vidaka were in the pre-fertilisation stage, and two of these showed damage by *P. wayi*. Those in the normal-nutfall, post-fertilisation stage numbered 1,476, and 129 (8·74 per cent.) of them showed damage by *P. wayi*. The remaining 17 were older nutlets, of which 5 showed damage by *P. wayi*.

From these figures it will be seen that the method advocated is to some

extent a compromise, but the extra accuracy that would be obtained by examining the fallen material more closely, to exclude all but a particular stage of development, would mean that, for the same cost, a smaller sample would have to be taken, so that what is now lost in lack of refinement of the technique is made up by the larger samples that can be examined.

It has been questioned whether the fallen vidaka should be picked from below selected palms, selected rows or groups of palms, or at random throughout the area. All these methods were tried, and the results did not differ significantly from each other.

In addition, the vegetation was cleared from a rectangular block of 20 palms in the centre of a 10-acre plot and all the fallen vidaka (which in such a cleared area could be found quite readily) collected daily. The results from this were compared with those from a thrice-weekly random collection in the remainder of the 10-acre plot. When the monthly totals are compared, there is no significant difference between the results but for batches representing shorter periods there may be wide variation. This is also true for individual batches from randomised collections, but the variation between individual batches from groups of pre-selected palms was much greater.

The variation amongst the daily collections from 20 palms was as follows. An average of 25 fallen vidaka was collected daily and the damage rate varied from nil (on two occasions) to 100 per cent. (on 45 occasions). The average damage rate was about 60 per cent. The reason for this extreme variation lies in the growth of the nuts in relation to the ecology of the area. It is the exception, rather than the rule, that *P. wayi* is distributed evenly all over a coconut plantation. The red tree-ant, *O. longinoda*, feeds on both the nymphs and adults of *P. wayi* (Way, 1951, 1953*a*, *b*; Vanderplank, 1953). A strong colony of *Oecophylla* completely protects the palm from *P. wayi* and the fruiting bodies that fall from such palms do so from natural causes, and none show insect damage. Weaker colonies of *Oecophylla* give a varying degree of protection, and are thus associated with a variable proportion of vidaka showing damage by *P. wayi*. In areas where the yellow "crazy" ant, *Anoplolepis longipes* (Jerd.), is well established, there are no *Oecophylla*, and in such areas *P. wayi* and the damage caused by it are evenly distributed over the plantations, with an occasional, exceptional palm on which no damage occurs. All such exceptional palms so far examined have been found to be frequented by one or more specimens of a species of green lizard (awaiting identification). Laboratory tests show that some individuals of this lizard will eat all stages of *P. wayi*, and it is considered that the lizard is responsible for protecting the fruits on the exceptional palms. When the lizards are removed, the palm becomes infested by *P. wayi* and the fruits damaged.

It is not possible to gather the fallen vidaka from any one particular palm, as the height from which they fall (varying from 15 to 90 ft.) results in their scattering over a distance greater than that between the palms. If collections were made from selected palms or rows of palms, the results might easily be biased as a result of movements and changes in the numbers of *Oecophylla*, even though the distribution of the latter was representative of the whole area at the time of selecting the palms. Moreover, the type of labour used for this work is best suited to carry out randomised collection, rather than to attempt to gather all the material from below pre-arranged palms.

The Vidaka Damage Rate in Relation to Populations of *P. wayi*.

Since the nymphs of *P. wayi* are wingless (Pl. XXIII, figs. 3 & 4) it should be possible to count or collect these and obtain some indication of the size of the population of the insect. However, owing to the height of the palms, and the cryptic colouring of the nymphs, this proves extremely difficult in practice.

Tables I and II give the numbers of nymphs of *P. wayi* observed on 12 palms in each of two areas at Chukwani, one of which (H) was left untreated, the other (I) being treated with an insecticidal spray at monthly intervals. The palms were climbed and searched at weekly intervals by two trained entomologists (F.L.V., E.M.T.). The Tables include also the corresponding V.D.R. determined one week later in the same area, but representing more than the 12 palms searched for *P. wayi*.

There was less variation in both the numbers of *P. wayi* observed and the V.D.R. in the untreated area (which was partly infested with *Anoplolepis*

TABLE I.

Population of *P. wayi* and vidaka damage rate, control area, Chukwani (H), 1954.

Y = Number of nymphs (all instars) of *P. wayi* found on 12 palms in given week.
X = Vidaka damage rate one week later.
N = Number of palms found to be infested with *P. wayi*.

Month	Week	Y + 1	N	X
March	1	18	9	75
	2	24	11	77
	3	22	10	84
	4	22	10	80
April	—	No data	—	—
May	1 & 2	9	6	68
	3 & 4	16	7	75
June	1	5	3	64
	2	7	3	58
	3	10	7	71
July	1	9	6	68
	2	8	6	66
	3	3	3	60
	4	3	3	61
	5	4	3	64
August ..	1	5	4	70
	2	5	4	74
	3	4	3	65
	4	15	6	78
September ..	1	12	7	80
	2	3	3	65
	3	2	2	58
	4	10	5	83
October ..	1	4	4	72
	2	5	2	62
	3	9	3	65
	4	5	2	58
November ..	1	3	2	61
	2	7	4	77
	3	3	2	82
	4	5	2	59

$\overline{X} = 69{\cdot}3$. $\overline{Y} = 7{\cdot}57$. $n = 30$.

Correlation coefficient $r = +0{\cdot}55$ ($P < 0{\cdot}01$, assuming the association to be linear).

longipes and partly with the *Pheidole–Oecophylla* complex) than in the experimental area. In each area, the two variables, numbers of nymphs of *P. wayi* and V.D.R., show a significant correlation. When the combined data from the two areas are shown on a graph (fig. 2), it is clear that they are not linearly

TABLE II.

Population of *P. wayi* and vidaka damage rate, experimental area, Chukwani (I), 1954.

Month	Week	Y + 1	N	X
March	1	2	1	30
	2	24	12	75
	3	12	9	66
	4	20	10	67
April	—	No data	—	—
May	1	5	2	23
	2	2	1	10
	3	2	1	12½
	4	2	1	8
June	1	No data	—	—
	2	1	0	5½
	3	1	0	3
	4	1	0	5
July	1	1	0	2½
	2	1	0	1½
	3	1	0	4½
	4	1	0	3
August ..	1	1	0	6½
	2	0*	0	0*
	3	4	2	6
	4	1	0	12
September ..	1	1	0	10½
	2	1	0	10
	3	1	0	57½
	4	1	0	42
	5	4	3	37
October ..	1	1	0	48
	2	1	0	36
	3	1	0	43
	4	1	0	8
November ..	1	5	3	38
	2	6	3	53
	3	12	4	56
	4	2	1	39

X, Y, N as in Table I.

* Since both X and Y were nil, this observation has been excluded from the calculations

$\overline{X} = 26{\cdot}4$. $\overline{Y} = 2{\cdot}84$. $n = 31$.

Correlation coefficient $r = +0{\cdot}70$ ($P < 0{\cdot}01$, assuming the association to be linear).

The marked falls in insect population and damage rates that are apparent in this Table (and also in Tables IV and VI–X) follow insecticidal treatment.

TABLE III.

Total numbers of nymphs (all instars) of *P. wayi* found and of palms searched, each week, and mean V.D.R. from a random collection over the whole area one week later (Kizimbani, 100-acre control plot).

Week ending (1956–57)	No. of nymphs found (n)	No. of palms searched (N)	N/n	No. of fallen vidaka examined	V.D.R.
13.x ..	10	100	10	307	58
20.x ..	25	200	8	653	61
3.xi ..	33	300	9	350	56
17.xi ..	41	310	8	345	53
24.xi ..	54	350	6	474	63
1.xii ..	39	360	9	756	58
8.xii ..	52	360	7	443	60
15.xii ..	23	320	14	341	56
22.xii ..	36	360	10	552	54
29.xii ..	20	270	14	547	50
5.i ..	20	350	17	527	44
12.i ..	15	360	24	873	42
19.i ..	41	360	9	1,159	49
26.i ..	14	240	17	1,239	46
1.ii ..	12	260	22	1,042	43
8.ii ..	4	180	45	1,459	53
16.ii ..	10	300	30	639	46
23.ii ..	19	360	19	1,329	44
2.iii ..	18	613	34	1,090	41
9.iii ..	15	933	62	649	29
16.iii ..	5	680	136	782	21
23.iii ..	5	290	58	1,277	36
30.iii ..	33	500	15	1,204	32

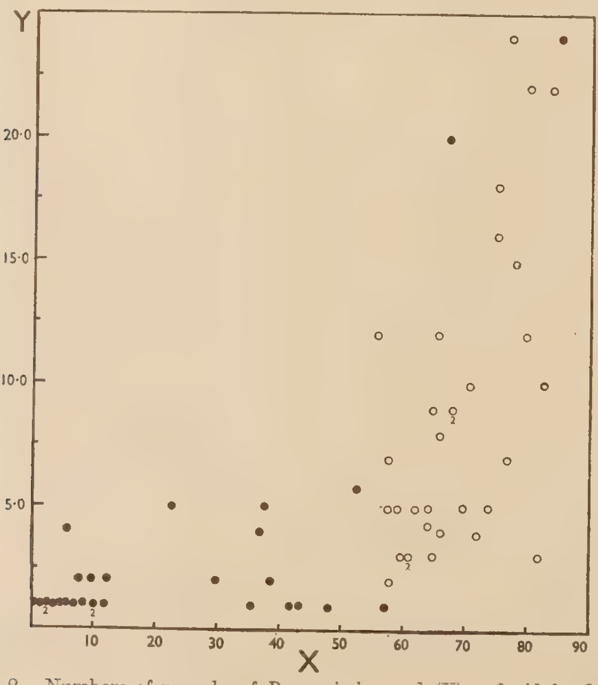


Fig. 2.—Numbers of nymphs of *P. wayi* observed (Y) and vidaka damage rate (X) for the same area one week later.
Open circles: Chukwani (H), control area.
Solid circles: Chukwani (I), experimental area.

associated, and if the data are corrected by a logarithmic conversion, the correlation just fails to reach significance. It seems probable that this reflects the paucity of data on numbers of *P. wayi* rather than a lack of association between the two variables.

Adults of *P. wayi* are very seldom seen, since they fly away when disturbed, but they may form a majority of the population, and they inflict the severest damage. First-instar nymphs do not cause any damage to the vidaka, and second-instar nymphs very little, so that the population of neither is directly related to the observed damage. In a population that has not been exposed to insecticidal treatment, each of these early instars probably represents a nearly constant proportion of the total population. In areas treated with an insecticide, this is not likely to be true, since a single application can destroy well over 90 per cent. of the population. Such areas are subsequently re-invaded by adults from the surrounding unsprayed areas, and since there will be few surviving natural enemies, and plenty of food, a large number of eggs will be laid; this results in the presence of large numbers of first- and second-instar nymphs concurrently with a low V.D.R. that reflects only the adult population present. This biases any data collected when a sprayed area is being re-invaded by *P. wayi*.

To obtain more data on the relation between populations of *P. wayi* and the damage they inflict, ten climbers were trained to search for *P. wayi*. Two areas

TABLE IV.

Total numbers of nymphs (all instars) of *P. wayi* found and of palms searched, each week, and mean V.D.R. from a random collection over the whole area one week later (Kizimbani, 100-acre treated plot).

Week ending (1956–57)	No. of nymphs found (n)	No. of palms searched (N)	N/n	No. of fallen vidaka examined	V.D.R.
13.x ..	25	250	10	298	53
20.x ..	5	250	50	433	32
27.x ..	5	250	50	318	32
3.xi ..	4	430	107	344	25
10.xi ..	1	240	240	511	21
17.xi ..	0	340	—	1,190	7
24.xi ..	0	390	—	480	1·9
1.xii ..	0	330	—	913	0·8
8.xii ..	2	360	180	588	3·7
15.xii ..	0	360	—	590	2·9
22.xii ..	2	360	180	666	6
29.xii ..	3	360	120	783	9
5.i ..	1	360	360	937	6
12.i ..	12 *a*	360	30	883	9
19.i ..	52 *b*	420	8	796	8
26.i ..	24 *a*	400	17	952	15
1.ii ..	1 *a*	400	400	764	16
8.ii ..	8	360	45	1,207	19
16.ii ..	7	780	110	837	10
23.ii ..	0	820	—	697	5·3
2.iii ..	28 *c*	360	13	742	7
9.iii ..	18 *a*	360	20	987	3·3
16.iii ..	4 *d*	360	90	998	0·8
23.iii ..	5	140	28	1,010	4·0

a All 1st or 2nd instar nymphs.
b 28 of these were 1st or 2nd instar nymphs.
c 10 of these were 1st or 2nd instar nymphs.
d 3 of these were 1st or 2nd instar nymphs.

TABLE V.

Numbers of late-instar nymphs of *P. wayi* and of palms searched, each week, and V.D.R. for the same sector one week later.

Week ending (1956–57)	No. of nymphs in given instar			Total nymphs (n)	No. of palms searched (N)	N/n	V.D.R.
	3rd	4th	5th				
20.x	2	—	2	4	80	20	53
27.x	9	—	—	9	500	56	32
3.xi	1	1	—	2	600	300	7
8.xii	2	—	—	2	1000	500	4
19.i	24	5	1	30	650	22	30
8.ii	5	2	—	7	900	129	8
16.ii	2	1	—	3	240	80	15
2.iii	13	4	1	18	480	27	43
23.iii	2	2	1	5	360	72	18
30.iii	12	1	1	14	940	67	19

Table V includes data given, in part, in Table IV, and also the results of additional observations made in the same sector of the experimental area on occasions when extra labour was available.

at Kizimbani, each of 100 acres, one of which was undergoing insecticidal treatment, the other being the control, were searched on alternate days, some 200 palms being climbed on each occasion. The data obtained from October 1956 to March 1957 are given in Tables III and IV. As in Tables I and II, there is much less variation in the figures obtained in the control area than in those for the experimental area, and both sets of data suggest that the relationship between the population of *P. wayi* and the V.D.R. is curvilinear, and it can, in fact, be shown to be logarithmic.

The data mentioned above were based on nymphs of all instars of *P. wayi* and the mean V.D.R. over the whole area. Since detailed records were kept it was possible to analyse these further. Table V gives these data, but with any first- or second-instar nymphs excluded, and also any week when no *P. wayi* were caught. The V.D.R. is based on the counts made one week later in the same sector of the experimental area as that in which the counts of nymphs were

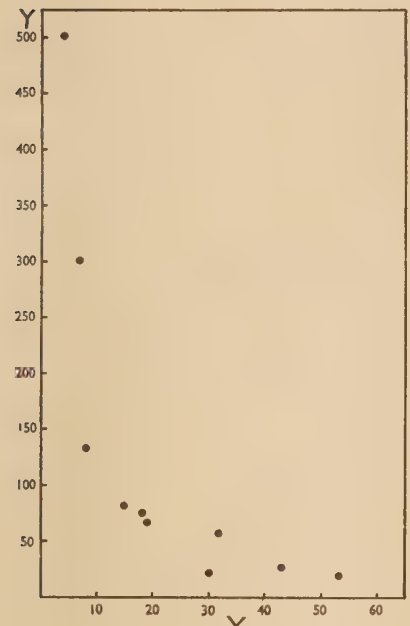


Fig. 3.—Numbers of palms searched to obtain one 3rd–5th-instar nymph of *P. wayi* (Y) and vidaka damage rate (X) for same sector one week later. Experimental area, Kizimbani (data from Table V).

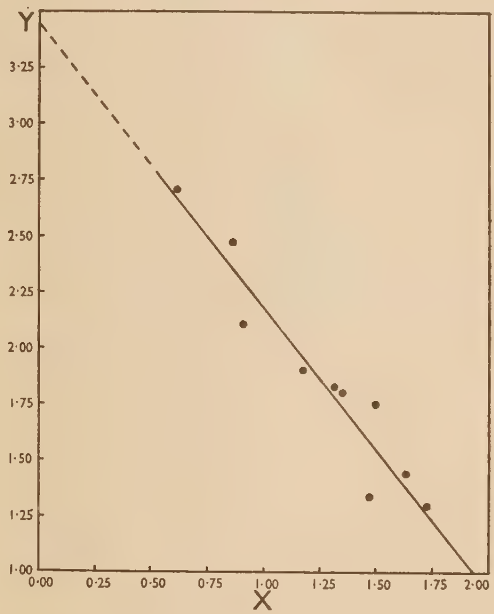


Fig. 4.—Data from Table V and text-fig. 3, converted to logarithms, with regression line Y = 3·43−1·26X, where X = log(V.D.R.) and Y = log(N/n).

made, and the density of the population of *P. wayi* is expressed as the number of palms searched per nymph found (N/n). When these data are plotted on a graph (fig. 3) they fall on a curve. If both quantities are converted to logarithms, the transformed data show a straight-line relationship (fig. 4), and the coefficient of correlation between X (= log V.D.R.) and Y (= log (N/n)) is $r = -0{\cdot}975$, which is significant.

TABLE VI.

Vidaka damage rate and yield, Mazizini (A), 1954–57.

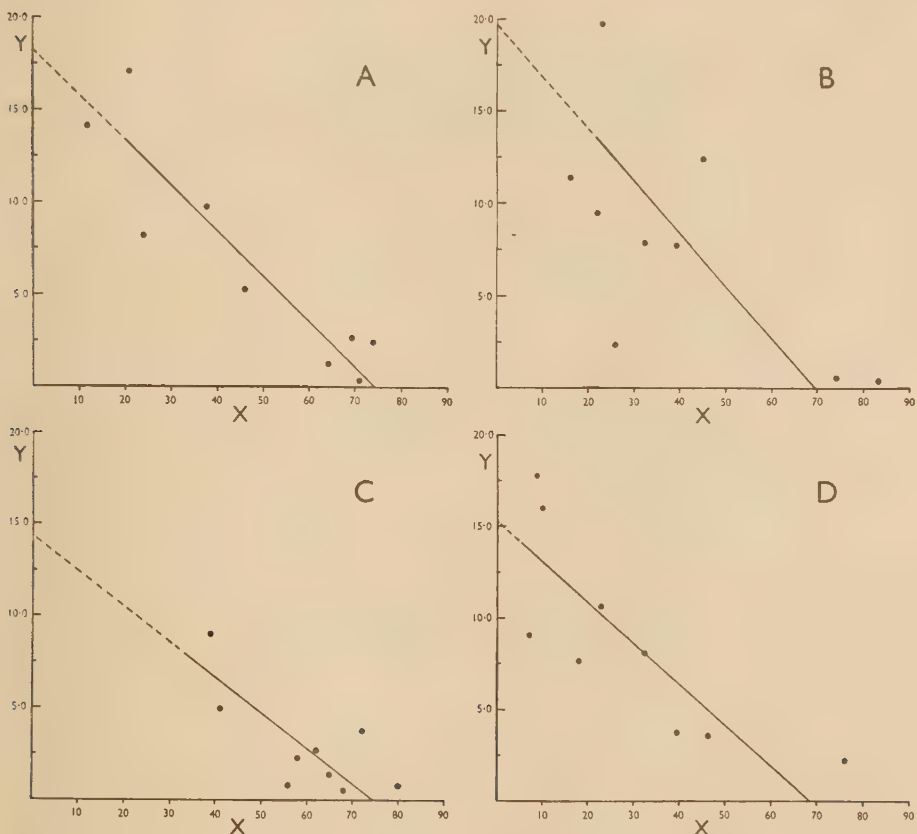
Months when vidaka were collected	Number of fallen vidaka collected		V.D.R. (X)	Harvesting (month in brackets)	Total yield (nuts)	Average nuts per palm (Y)
	Total	No. with lesions caused by *P. wayi*				
1954				1955		
Feb., March, April ..	3,059	1,401	46	First (Feb.)	1,855	5·4
May, June, July ..	2,302	491	21	Second (May)	5,932	17·3
Aug., Sept., Oct. ..	1,002	237	24	Third (Aug.)	2,772	8·1
Nov., Dec., Jan. 1955 ..	925	640	69	Fourth (Oct.)	939	2·7
1955				1956		
Feb., March, April ..	568	420	74	First (Jan.)	830	2·4
May, June, July ..	678	257	38	Second (April)	3,384	9·8
Aug., Sept., Oct. ..	442	56	12	Third (July)	4,870	14·2
Nov., Dec., Jan. 1956 ..	937	598	64	Fourth (Oct.)	451	1·3
1956				1957		
Feb., March, April ..	1,726	1,228	71	First (March)	187	0·5

Total number of palms in plot: 343. $\bar{X} = 46{\cdot}6$. $\bar{Y} = 6{\cdot}8$.

From the calculated regression of Y on X (*i.e.*, $Y = 3{\cdot}43 - 1{\cdot}26X$), the following association between V.D.R. and observed density of population of 3rd- to 5th-instar nymphs of *P. wayi* would be expected:—

Number of palms searched to find one nymph	V.D.R.
10	84
18	50
32	32
56	21
100	13
320	5·6
1,000	2·4

These figures suggest that when damage due to *P. wayi* is high, actual counts of 3rd- to 5th-instar nymphs will give the most accurate assessment of the



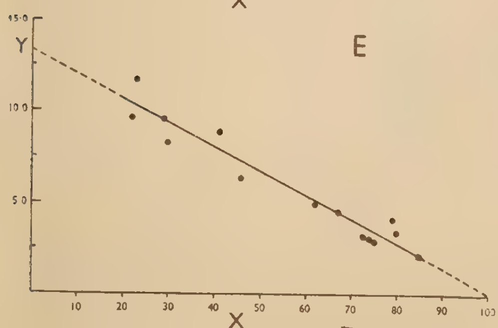


Fig. 5.—Regression of yield, expressed as mean number of nuts per gathering (Y), on vidaka damage rate (X).
A, Experimental plot, Mazizini (A); B, Experimental plot, Mazizini (B); C, Experimental plot, Mazizini (C); D, Experimental plot, Chukwani (I); E, Experimental plot, Chukwani (L).

TABLE VII.

Vidaka damage rate and yield, Mazizini (B), 1954–57.

Months when vidaka were collected	Number of fallen vidaka collected		V.D.R. (X)	Harvesting (month in brackets)	Total yield (nuts)	Average nuts per palm (Y)
	Total	No. with lesions caused by *P. wayi*				
1954				1955		
Feb., March, April ..	2,501	1,128	45	First (Feb.)	3,473	12·4
May, June, July ..	1,734	392	23	Second (May)	5,517	19·7
Aug., Sept., Oct. ..	1,158	189	16	Third (Aug.)	3,133	11·3
Nov., Dec., Jan. 1955 ..	1,310	506	39	Fourth (Oct.)	2,131	7·7
1955				1956		
Feb., March, April ..	1,382	306	22	First (Jan.)	2,617	9·4
May, June, July ..	840	271	32	Second (April)	2,180	7·8
Aug., Sept., Oct. ..	559	145	26	Third (July)	671	2·4
Nov., Dec., Jan. 1956 ..	848	631	74	Fourth (Oct.)	147	0·5
1956				1957		
Feb., March, April ..	1,270	1,054	83	First (March)	218	0·8

Total number of palms in plot: 278. $\overline{X} = 41·0$. $\overline{Y} = 8·01$.

TABLE VIII.

Vidaka damage rate and yield, Mazizini (C), 1954–57.

Months when vidaka were collected	Number of fallen vidaka collected		V.D.R. (X)	Harvesting (month in brackets)	Total yield (nuts)	Average nuts per palm (Y)
	Total	No. with lesions caused by *P. wayi*				
1954				1955		
Feb., March, April ..	1,984	1,146	58	First (Feb.)	1,098	2·3
May, June, July ..	2,000	783	39	Second (May)	4,304	9·1
Aug., Sept., Oct. ..	1,146	473	41	Third (Aug.)	2,322	5·0
Nov., Dec., Jan. 1955 ..	1,163	728	62	Fourth (Oct.)	1,236	2·7
1955				1956		
Feb., March, April ..	1,060	763	72	First (Jan.)	1,773	3·8
May, June, July ..	1,011	658	65	Second (April)	655	1·4
Aug., Sept., Oct. ..	607	339	56	Third (July)	395	0·8
Nov., Dec., Jan. 1956 ..	848	680	80	Fourth (Nov.)	355	0·8
1956				1957		
Feb., March, April ..	1,964	1,331	68	First (March)	297	0·6

Total number of palms in plot: 471. $\bar{X} = 60{\cdot}1$. $\bar{Y} = 2{\cdot}94$.

TABLE IX.

Vidaka damage rate and yield, Chukwani (I), 1954–57.

Months when vidaka were collected	Number of fallen vidaka collected		V.D.R. (X)	Harvesting (month in brackets)	Total yield (nuts)	Average nuts per palm (Y)
	Total	No. with lesions caused by *P. wayi*				
1954				1955		
Feb., March, April ..	1,881	192	10	First (Jan.)	9,600	16·0
May, June, July ..	1,546	146	9	Second (April)	14,220	17·8
Aug., Sept., Oct. ..	981	227	23	Third (July)	8,490	10·6
Nov., Dec., Jan. 1955 ..	1,144	365	32	Fourth (Oct.)	6,580	8·2
1955				1956		
Feb., March, April ..	1,291	92	7	First (Jan.)	7,320	9·1
May, June, July ..	1,334	239	18	Second (May)	6,110	7·6
Aug., Sept., Oct. ..	1,012	395	39	Third (Aug.)	2,960	3·7
Nov., Dec., Jan. 1956 ..	1,359	626	46	Fourth (Nov.)	2,860	3·6
1956				1957		
Feb., March, April ..	1,310	998	76	First (Feb.)	1,870	2·3

Total number of palms in plot: 800. $\bar{X} = 29{\cdot}0$. $\bar{Y} = 8{\cdot}8$.

population, but when the damage rate is below 20 per cent., the V.D.R. itself will give the most reliable assessment of the population, since the population density giving rise to such rates of damage is so low that its accurate determination is unlikely to be possible. It is these low populations that are most important in experimental control work; for example, the V.D.R. in the 100-acre experimental plot at Kizimbani (see Table IV) fell as low as 0·8 per cent. on two occasions, when based on a randomised sample of 913 and 998 fallen vidaka, respectively.

The Vidaka Damage Rate in Relation to Final Yields.

Data on V.D.R. and yields have been collected from several different experimental plots and control areas. The data from the control areas are too uniform to give rise to significant correlations. Each of the five experimental plots was treated with insecticides during part of the period of observation, and the data are given in Tables VI to X. A quarterly estimate of the V.D.R. was obtained from the number of vidaka that showed lesions amongst the total vidaka collected during the 3-month period, and this was compared with the figure for yield obtained from the harvesting made approximately one year later. The relationship between V.D.R. and yield is linear (fig. 5), and not logarithmic as was found with observed numbers of *P. wayi* and V.D.R.

The vidaka stage, which covers the first three months of the life of the fruiting body (dated from the opening of the spadix), is most sensitive to *P. wayi*. As the nutlet matures, it becomes less likely to be shed as a result of damage by *P. wayi*, although this will occur if the damage is severe enough. The nutlet is exposed to possible damage from *P. wayi* for eight to nine months after passing the vidaka stage, but this long exposure to damage is offset by the increased resistance of the older nut. Thus the V.D.R. gives an indication of the expected loss of yield 10 to 12 months later. The age at which the nuts are harvested in Zanzibar is variable, because they are picked at roughly three-monthly intervals * and often some are picked a month before they are fully mature.

This method of forecasting yield breaks down if *P. wayi* is controlled for, say, three months, so that a very low V.D.R. is recorded over that period, and then control is relaxed, so that there is then an increase in the population of *P. wayi*. Under these circumstances, the population that is built up again will destroy a high proportion of the nutlets saved during the three months of effective control.

The ideal way to obtain accurate data on this subject would be to have a number of experimental plots where the V.D.R. could be kept approximately constant at a different given level in each plot for 18 months to two years. Since this has not been possible, the data presented here are the best available to date. Table XI shows, for each of the areas from which the data in Tables VI to X were obtained, the essential data for the regression, $Y = a + bX$, of yield (Y) on V.D.R. (X), together with the values of the correlation ratio r, and the number of pairs of observations (n) on which it is based. The value of r is significant in every case.

From Table XI it will be noticed that the slope of the regression line (b) changes with different areas and expected crops.

The maximum expected yield will be that when the V.D.R. is nil, and it is thus given by the constant a in Table XI. That from Mazizini (B) is 19·8 nuts per gathering (or 79·2 nuts per palm per annum), whereas in Chukwani (L) it is only 13·65 nuts per gathering (54·6 nuts per palm per annum). Since the yields from each palm in this plot have been recorded separately it is possible to

* Harvesting was carried out by the Department of Agriculture as and when labour was available, at intervals that sometimes appear to be more, or less, than three months in Tables VI–IX, according to the day of the month on which the nuts were gathered.

TABLE X.

Vidaka damage rate and yield, Chukwani (L), 1953–56.

Months when vidaka were collected	Number of fallen vidaka collected: Total	No. with lesions caused by *P. wayi*	V.D.R. (X)	Harvesting (month in brackets)	Total yield (nuts)	Number of palms	Average nuts per palm per quarter (Y)
1953				1954			
Feb., March, April	910	421	46	First (Jan.)	3,983	626	6·4
May, June, July	845	525	62	Second (April)	3,055	625	4·9
Aug., Sept., Oct.	657	482	73	Third (Aug.)	2,021	625	3·2
Nov., Dec., Jan. 1954	892	756	85	Fourth (Nov.)	1,332	624	2·1
1954				1955			
Feb., March ..	451	184	41	First (Jan.)	3,718	624	8·9*
April, May	787	235	30	Second (March)	3,467	623	8·3*
June, July	841	196	23	Third (May)	4,843	621	11·7*
Aug., Sept.	563	162	29	Fourth (July)	3,987	620	9·7*
Oct., Nov.	446	100	22	Fifth (Sept.)	4,040	618	9·7*
Dec., Jan. 1955 ..	556	373	67	Sixth (Nov.)	1,830	615	4·5*
1955				1956			
Feb., March, April ..	1,190	942	79	First (Feb.)	2,530	614	4·1
May, June, July ..	591	439	74	Second (May)	1,890	612	3·1
Aug., Sept., Oct. ..	497	375	75	Third (July)	1,690	612	2·8
Nov., Dec., Jan. 1956	607	486	80	Fourth (Oct.)	2,020	610	3·3

* Since these harvestings were made at intervals of two months only and the others on the more usual quarterly basis, the means have been corrected to show the equivalent yield per quarter.

Total number of palms per plot: 626 (at start)–610 (at finish). $\overline{X} = 55{\cdot}4$. $\overline{Y} = 5{\cdot}91$.

analyse the data further. Of the 626–615 palms in the area, 74 had strong colonies of *Oecophylla* nesting in the leaves during 1954 and 1955. These palms averaged 70·3 nuts per palm per annum during these two years, which is well above the average figure for the whole plot obtained by extrapolation from the regression. Although the yields of the palms without strong *Oecophylla* colonies are available from the data, no separate records of V.D.R. were kept, so that it

TABLE XI.

Correlations and regression data from five experimental plots.

Table	Plot	r	n	a	b
VI	Mazizini (A)	−0·938	9	18·3	−0·248
VII	Mazizini (B)	−0·864	9	19·8	−0·287
VIII	Mazizini (C)	−0·700	9	14·4	−0·192
IX	Chukwani (I)	−0·824	9	15·75	−0·242
X	Chukwani (L)	−0·984	14	13·65	−0·141

is not possible to correlate yield and V.D.R. for such palms. Data are still being collected on this point, with a view to publication later.

In general, the above data and calculations show that the V.D.R. is a good measure of the yields to be expected, provided that the rate does not rise unduly in the interim, while the nuts are maturing.

Summary.

A method of estimating the damage inflicted on the developing fruit of the coconut palm by *Pseudotheraptus wayi* Brown is needed in order to assess the efficacy of measures for the control of this Coreid. The insect lives in the crown of the palm, populations are small in relation to the damage they cause, the adults take wing readily and the nymphs are agile and secretive. Direct estimation of populations by hand-collection, trapping, the use of knockdown sprays and marking-recapture methods, using paints or radioactive materials, were all unsuccessful, and indirect methods of estimation were therefore studied.

The growth, flowering and fruiting habits of the coconut palm are described. There is a single growing point, at which the leaves are produced in succession. From 12 to 18 inflorescences are formed each year; each is borne in a leaf axil and carries male flowers distally and female flowers proximally; the latter open, and are fertilised, almost together, after all the former have fallen off, and some 3–4½ weeks after the inflorescence has emerged from its spadix. All subsequent stages in the development of the fruiting body are dated from the latter event.

The young nut at first elongates rapidly and in the first six months attains over 80 per cent. of its final length; it is ripe at about a year.

In the absence of damage by insects, from 20 to 80 per cent. of the fruiting bodies are shed as nutlets, 1–2 weeks after fertilisation, the proportion depending on the variety of the palm and being less in those that bear few flowers and large nuts, but very few are shed at any other stage of their development. When an adult or a late-instar nymph of *P. wayi* feeds upon a developing fruiting body a characteristic lesion develops at the site of the puncture, which is concealed by the calyx, and if the fruiting body is less than three months old at the time

(in which case it is locally termed a *kidaka*, plural *vidaka*) it is normally shed 4–7 days later. As the nut develops, it becomes less likely to be shed following attack by *P. wayi*, although the lesion formed may be invaded by fungi or by the weevil, *Diocalandra frumenti* (F.). Fruiting bodies attacked by the latter insect cease growth but are not shed. Experiments and field observations show that where damage by *P. wayi* is prevalent, a proportion of the vidaka are shed in the pre-fertilisation stage, even though they show no evidence of attack by the insect. The extent and implications of this phenomenon are not yet understood.

Fallen vidaka rot quickly and those that are found will reflect the damage that was inflicted 7–10 days previously. By collecting a sample of freshly fallen vidaka, removing the calyces and determining the percentage of them that shows damage by *P. wayi*, a measure is obtained that is termed the Vidaka Damage Rate (V.D.R.). The method advocated is to collect at random and at weekly intervals a sample of at least 100 vidaka per ten acres, excluding any with an overall length exceeding three inches. This size is reached at about $2\frac{1}{2}$ months; older fallen nutlets invariably show damage from *P. wayi* or other causes. No significant differences have been found between values of the V.D.R. based on such collections and those based on collections from below individual palms, or rows of palms, taken at random. No significant difference was found between vidaka in the pre-fertilisation stage and those in the stage at which normal nutfall occurs as regards the proportion showing damage by *P. wayi*, and the former are therefore not excluded.

Comparison of the numbers of nymphs of *P. wayi* found by two trained entomologists at weekly intervals on 12 palms in each of two areas, one of which was treated with an insecticidal spray at monthly intervals and the other left untreated, and the V.D.R. determined a week later in the same area but on a larger sample of palms, showed a curvilinear association between the two quantities; the association between the logarithms of the quantities was linear but the correlation was not quite significant. In more detailed investigations, two 100-acre areas were used, one of which was undergoing insecticidal treatment, and in each a large but variable number of palms (from 100 to over 900) was examined during each week over a period from mid-October 1956 to the end of March 1957 by a team of climbers who had been trained to search for *P. wayi*. There was less variability in the data from the control than from the treated area; the latter showed a curvilinear relationship between the observed population of nymphs of *P. wayi* and the V.D.R. from the whole area one week later, but the correlation between the logarithms of the two variables was not significant.

If counts of first- and second-instar nymphs, which cause very little damage, were excluded from the data, together with any week in which no individuals were recorded, and the values of the V.D.R. were computed from that part of the area in which the insects were counted, then, when both variables were converted to logarithms, the transformed data showed a straight-line relationship with a highly significant correlation coefficient of $-0{\cdot}975$. The regression equation indicates that where the number of palms that it would be necessary to search in order to find one 3rd- to 5th-instar nymph is 10, 100 or 1,000, the corresponding value of the V.D.R. would be 84, 13 or 2·4, respectively. It is concluded that where the V.D.R. is below 20, the population density giving rise to such a rate of damage is so low that its accurate determination by direct counts is unlikely to be possible.

Data on V.D.R. and yield were collected from a number of experimental plots and control areas; values from the latter were too uniform to give rise to significant correlations, but when a quarterly estimate of the V.D.R. in an experimental area, obtained from the totals of damaged and of undamaged fallen vidaka collected during successive three-month periods, was compared with the figure for yield obtained from harvesting the same area during the corresponding

quarter the following year, a linear relationship was found between yield and V.D.R., the coefficient of correlation being significant in each of the five areas considered, and ranging from $-0{\cdot}7$ to $-0{\cdot}984$, and the values of a and b in the regression equation $Y = a + bX$, where Y is the yield in nuts per palm per harvesting and X is the quarterly value of the V.D.R., ranged from 13·65 to 19·8, and $-0{\cdot}141$ to $-0{\cdot}287$, respectively. It is concluded that the V.D.R. is a good measure of expected yield, provided that the rate does not rise unduly in the interval between assessment and harvest; in such circumstances, the increased population of *P. wayi* that is reflected in the increased V.D.R. may damage the nuts at a later stage of their development and so reduce the yield below that expected.

Acknowledgements.

My thanks are due to Mr. A. K. Briant, O.B.E., Director of Agriculture, Zanzibar and to the Isotope Information Office of the Atomic Energy Research Establishment, Harwell, for their helpful criticism, and to the latter, also, for the supply of ^{32}P and ^{35}S and for permission to publish the results of experiments with these materials.

Many people have co-operated in this work, and my thanks are due to Mrs. E. M. Bowler (née Miss E. M. Tait), Dr. R. A. E. Galley, Mr. G. E. Tidbury and Mr. K. Wilson-Jones; to Mr. K. S. Hocking, Mr. K. S. McKinlay, Mr. D. Yeo and other members of the Colonial Pesticides Research Unit, Arusha; to Miss Rabia M. Hamdania and Mr. L. J. Stevens; and last, but not least, to the staff in Zanzibar who have done the hard manual work involved.

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FIG. 1. Kidichi experimental area, Zanzibar, showing 70-ft. extending ladder against a 40-ft. coconut palm.

FIG. 2. Newly opened inflorescence of coconut palm, showing male (distal) and female (proximal) flower buds.

FIG. 3. Inflorescence showing open female flowers; all male flowers have abscissed.

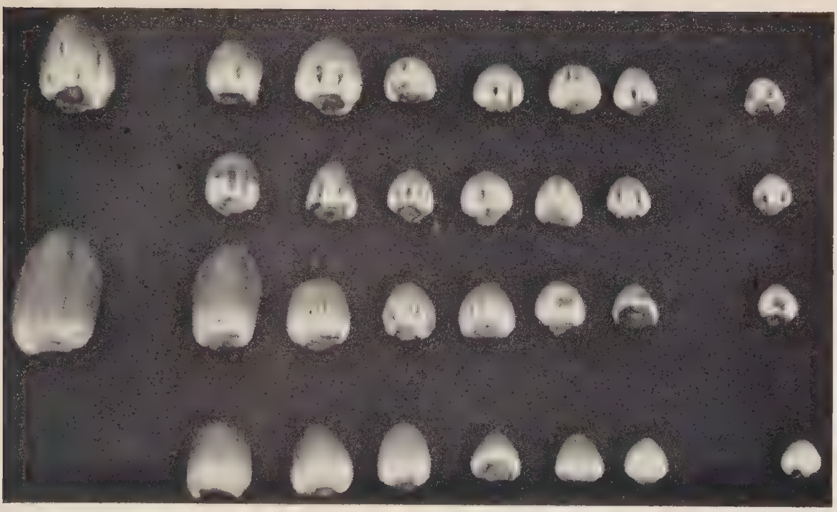

FIG. 1. Fallen fruiting bodies damaged by adults of *P. wayi* (row 1, top), by 4th - or 5th-instar nymphs (row 2), and by late 2nd- or 3rd-instar nymphs (row 3), or undamaged (row 4, bottom). Column 1, vitale ; cols. 2 - 7, vidaka (soon after flowering); col. 8, vidaka (pre-flowering). All calyces removed.

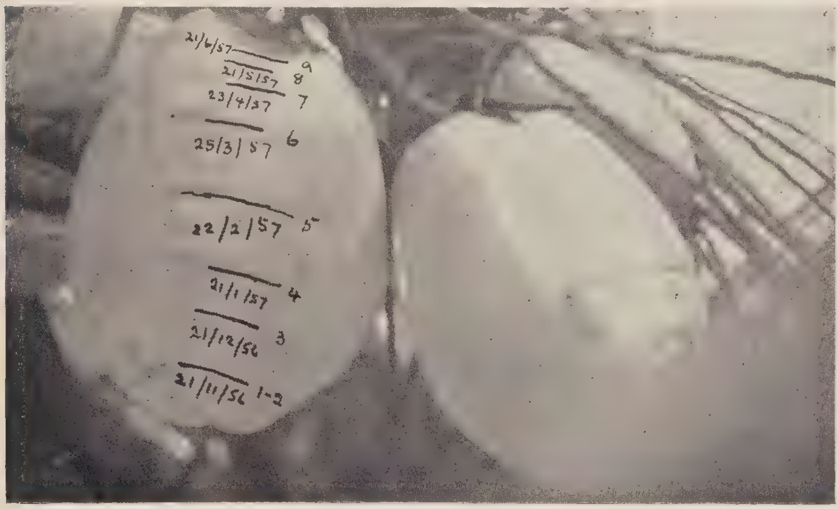

FIG. 2. Coconuts 9 months old, showing impressions, made at monthly intervals, marking edge of calyx (inked-in at left).

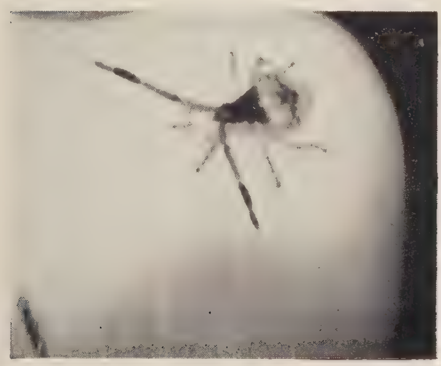

FIG. 3. Nymph of *P. wayi*, 3rd - instar, on surface of coconut.

FIG. 4. Nymph of *P. wayi*, 4th - instar, on surface of coconut.

PRELIMINARY NOTE ON A METHOD FOR THE DIRECT ESTIMATION OF POPULATIONS OF *PSEUDOTHERAPTUS WAYI* BROWN ON COCONUT PALMS.

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The Coreid bug, *Pseudotheraptus wayi* Brown, is a serious pest of coconut palms in East Africa, Zanzibar and neighbouring islands. The adults and nymphs, in feeding, destroy many flowers, and cause necrotic lesions to develop upon young nuts, which then fall off before they can mature; even somewhat older nuts are not immune to attack and many that do eventually mature are undersized and give poor yields of copra. Way (1953*a*) showed that the loss of crop in this fashion was probably very considerable, and this has been confirmed by later work (Vanderplank, unpublished). The insect has been described by Brown (1955).

Attempts at control have, hitherto, been assessed in terms of the effects upon final yields of the damage to flowers and young nuts, particularly those that fall to the ground. In both these techniques there is a considerable interval of time before the effects of control measures appear: about a year in the case of records of final yields, and a few weeks for records of damage to young nuts. In 1955, the need arose for a rapid assessment of the effect of insecticidal applications and it was considered worthwhile to investigate if this was possible by means of counts of numbers of *Pseudotheraptus*.

The Method of Searching.

The palms were searched by African assistants, who climbed in their traditional fashion using a loop of rope to join the feet together. A crown was searched systematically by progressing from spadix to spadix, and a complete search took 5–10 minutes, the exact period depending upon the extent of the crown and upon the individual climber. The insects were carefully placed in small specimen tubes and lowered to the ground with a fine string; there the nymphs were classified into instars, and the insects were then returned to the crowns. Very few adults were seen or captured, probably because they are able to fly.

Many palms were infested with *Oecophylla longinoda* (Latr.), an important ant predator of *Pseudotheraptus* (Way, 1953*b*). Although it is important to know what proportion of palms are protected in this way, it was considered unwise to include such palms in the counts even though *Pseudotheraptus* was found in two of them; climbing these ant-infested palms is in any case an uncomfortable experience and is not willingly undertaken. There was also a small number of stunted or immature palms, and these were also excluded from the counts.

The observations were made in a well-maintained plantation on Mafia Island, just off the east coast of Tanganyika. Five areas were chosen and intensive searches were made during the period from mid-January to mid-February 1956. Four of the areas were then treated with insecticides. The effect of these applications will be discussed in a later paper; here it is proposed to give data showing that the counting technique is likely to be a valuable additional tool in the study of this pest.

Results.

For completeness, the proportions of the numbers of palms protected by *Oecophylla* are given in Table I, which also records the small proportion of stunted or immature palms. Preliminary catches indicated that an average of one nymph was caught for each palm that was searched, and it therefore seemed reasonable that samples of approximately 100 palms should be taken.

TABLE I.

The incidence of *Oecophylla longinoda* in five experimental areas on Mafia Island during January and February 1956.

Area	No. of palms	Percentage of palms		
		Infested with *Oecophylla*	Under-developed	Climbed
1	580	32	3	65
2	412	6	4	90
3	439	13	5	82
4	415	34	3	63
5	256	39	2	59

Attempts were made to take one such sample from an area in one day. This was possible for most of the latter part of the period, but in January heavy rain interfered with the work and the earlier samples were therefore usually taken over two or three consecutive days. All the searchers concentrated on one area at a time, but there were some changes of staff from day to day.

No palm was searched more than once during the period covered by the records. Ideally, palms should have been selected at random from an area, but this would have greatly increased the problem of supervision, and would also have made it difficult to investigate certain facets of the subsequent insecticidal applications. The palms in a sample were therefore selected in rows and successive samples formed a somewhat irregular progression across the area. It is perhaps pertinent to point out that this sampling procedure would be likely to yield higher variations between catches of successive samples than would a method in which palms were randomly chosen.

During a period of about four weeks, up to four samples were taken in each area. They are summarised in Table II, where the catches for each area are entered in chronological order. The total nymphal populations, and the proportions of them in the various stages, are sufficiently consistent to suggest that the searching technique may give reproducible results, and thus be of considerable value as a means of assessing the results of control measures. There are fewer late-instar nymphs, and larger samples would be required to obtain reasonably consistent figures for them.

The possibility that individual searchers vary considerably in their ability to find and capture the nymphs is of obvious importance. At the beginning of January 1956, only three individuals had had any previous experience of catching, and for the period covered by Table II, the catches made by two of them were higher than those of any other searcher. After a very few weeks, however, the

TABLE II.

Catches of nymphs of *Pseudotheraptus wayi* in five experimental areas on Mafia Island during January and February 1956, expressed as numbers per 100 palms.

Area	No. of searched palms	Number of nymphs in each instar per 100 palms					
		1st	2nd	3rd	4th	5th	Total nymphs
1	86	78·1	17·4	11·6	4·6	2·3	114
	85	121·6	17·7	11·8	4·7	1·2	157
	84	72·6	25·0	8·3	5·9	1·2	113
	122	66·0	23·0	4·1	3·3	0·0	97
2	138	51·3	13·8	12·2	4·3	1·4	83
	90	75·1	18·9	7·8	2·2	0·0	104
	113	49·1	25·7	7·9	4·4	0·9	88
3	79	83·2	22·8	13·9	10·1	0·0	130
	72	66·8	11·1	6·9	4·2	0·0	89
	109	58·8	11·0	7·4	1·8	0·0	79
	102	52·4	13·7	5·9	0·0	1·0	73
4	61	87·2	39·0	9·8	0·0	0·0	136
	85	68·8	20·0	4·7	3·5	0·0	97
	113	86·2	36·5	8·7	2·6	0·0	134
5	102	64·6	12·7	5·9	7·8	0·0	91
	113	110·1	36·0	12·4	3·6	0·9	163
	101	103·6	48·5	12·9	2·0	1·0	168

catches became more uniform, and for the period March to May 1956 there was only a two-fold variation between those of the best and worst searchers. The details are given in Table III.

Crude attempts were made to assess the true populations of nymphs. Insects were collected from several palms and then placed, in groups of approximately

TABLE III.

Comparable daily catches for the various searchers during different periods.

Searcher	Daily catch of *Pseudotheraptus*	
	Jan.–Feb.	March–May
1*	24	6·0
2*	21	6·3
3*	10	4·4
4	6	—
5	13	4·7
6	8	3·6
7	6	3·1
8	12	4·5
9	10	6·9
10	12	5·3
11	7	4·2
12	5	4·7
13	13	6·4

* Climbers with some previous experience of searching.

10 per palm, into palms that had previously been exhaustively searched. On the following day, each of these palms was searched in the normal way; the nymphs captured were removed, and immediately afterwards a second search of each palm was made by a different climber. Recoveries of nymphs varied considerably from palm to palm, and only total releases and recaptures are given in Table IV. On two occasions the nymphs were marked with white oil paint (artists' colours), and there was some suggestion that too much paint reduced the possibility of recapture. About one-quarter of the nymphs was found in the first search, and the second search gave a further 10 per cent. or so. Had all nymphs been equally available at all times, the second catch should have been about double this percentage, so it might be that only a proportion of the population is readily caught

TABLE IV.

Recoveries of nymphs (all instars) 24 hours after release.

Month	Number released	Number recaptured in successive searches		Remarks
		1st search	2nd search	
Feb.	104	25	12	marked
	60	9	2	marked heavily
	60	17	7	unmarked
	14	5	2	unmarked
May	100	25	10	unmarked

at any one time. On the other hand, the activities of the first climber may easily have upset the normal pattern of behaviour and have driven many of the remaining nymphs into hiding.

The recapture technique is admittedly very crude, and will need considerable refinement to allow for such factors as mortality between release and recapture, but the figures of Table IV suggest that roughly one-quarter of the nymphal population in a palm was being caught in the routine searching.

Discussion.

It appears that reliable counts can be obtained with samples of approximately 100 palms, and that with very little experience individual searchers are able to get gratifyingly similar catches. For measuring the effect of insecticidal applications it would probably be wise to increase the sample size for counts made immediately following a treatment, and this is particularly true if interest is centred upon the older instars. The technique has certain disadvantages, however. One climber cannot deal happily with more than 15–20 palms in a day, so that a relatively large staff is required for extensive investigations. It is too dangerous to climb palms when they are wet, and this might interfere with the collection of records during periods of heavy and sustained rain, although this was not in fact found to be a serious problem during the heavy rains of 1956, when the records were only slightly disrupted. It is also not known if there is a subjective influence acting upon the searchers to give a non-linear relationship

between the catches and the true population. The unit of search is effectively a spadix, however, and since even in quite highly infested areas the number of nymphs caught is much less than the number of spadices, the searcher is usually "disappointed" in each unit search; it seems improbable, therefore, that changes in the level of infestation will have any marked effect upon his mental attitude. Finally, the catches are only of nymphs, and can give no direct knowledge of adult populations or of the effect upon them of insecticidal applications.

It seems improbable that the late-instar nymphs are less easy to find than the younger ones, and the data of Table II, combined with details of the life-history given by Way (1953*a*) and Tait (1954), suggest that there is a very high rate of mortality among the nymphs. A somewhat theoretical calculation, based upon the assumption of random death among the first- and second-instar nymphs, suggests that the rate of mortality decreases with increasing age of the nymph, although this conclusion is somewhat suspect because it is probable that some second-instar nymphs were erroneously recorded as first-instar. It does seem very likely, bearing in mind the relative lengths of the nymphal and adult periods, that the adults are much rarer than the nymphs.

TABLE V.

A test of the hypothesis that the nymphs are randomly distributed among the palms.

No. of nymphs caught	No. of palms having a given no. of nymphs		x	x^2	$\frac{x^2}{m}$
	Observed (x + m)	Calculated (m)			
0	711	443	+ 268	71800	162
1	230	482	− 252	63300	131
2	168	263	− 95	9010	34·3
3	91	95·5	− 4·5	20	0·2
4	47	25·4	+ 21·6	466	18·3
>4	70	8·2	+ 61·8	3819	466

Average catch per palm = 1·09. χ^2 = 812. d.f. = 4.

For four degrees of freedom, χ^2 is only 18·5 at the level of significance P = 0·001, and the distribution is therefore almost certainly non-Poissonian and non-random.

If the nymphs were distributed at random among the palms, it would be reasonable to expect the catch per palm to be distributed according to a Poisson distribution. This hypothesis can be tested using a χ^2 test. A large sample of individual catches per palm is so analysed in Table V, and the evidence points almost conclusively to a non-random distribution. There are too many *nil* catches, too few of magnitude 1 or 2, and too many of a magnitude greater than 3, and this suggests that the nymphs are concentrated in certain palms. For this there are a number of plausible and likely reasons: there may be fewer adult females than there are palms, and a female may tend to stay long enough in a certain palm to lay several eggs; or particular palms may be preferred by the females; or there may be a more extensive predation than is indicated by the counts of palms infested with *Oecophylla*.

Summary.

A technique is described for counting the numbers of *Pseudotheraptus wayi* Brown on coconut palms, on which this Coreid is a serious pest in East Africa, Zanzibar and the neighbouring islands. The crown of each palm is systematically searched by an African assistant, the insects collected being classified by instars and then replaced. The adults can fly and very few are seen or captured.

Palms were examined by a team of searchers in five areas in a well-maintained plantation on Mafia Island, 3–4 separate samples, each of 61–138 palms, being taken in each area between mid-January and mid-February 1956. In all, 13 searchers participated, but not all were used on the same day; when they had become experienced their daily catches were of comparable size.

The total nymphal populations, and the proportions of them in the various stages, are sufficiently consistent to suggest that the searching technique may give reproducible results, and thus be of considerable value as a means of assessing the results of control measures.

The average catch was about one nymph for each palm that was searched, and recaptures from known numbers of bugs liberated indicated that about one quarter of the population present was being found. The nymphal population is not distributed at random among the palms.

Acknowledgements.

The authors are very grateful to many people for their help, and especially to Mrs. O. Cluer, who very competently supervised the African assistants and collected much of the data. The climbers worked well, often under very trying conditions. Mr. H. J. Stanley, Jr., owner of the plantation, was very actively interested in the work, and his manager, Mr. R. Cluer, was very helpful. We have drawn freely from many unpublished reports of Dr. F. L. Vanderplank.

The costs of the work were met in various ways. Mr. Stanley generously paid most of the African staff, and other expenses were met by the Department of Agriculture, Tanganyika, or from funds made available from the Colonial Development and Welfare Fund.

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SYSTEMATIC NOTES ON SPECIES OF *CALLOSOBRUCHUS* OF ECONOMIC IMPORTANCE.

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(Plates XXIV & XXV.)

The "Cowpea Weevil", *Callosobruchus chinensis* (L.), has become dispersed through the medium of commerce, and now breeds throughout most of the tropics and sub-tropics. It is a very variable species and it is not surprising, therefore, that it has been described a number of times under different names. Other closely related species have been confused with it and some of them, notably *C. rhodesianus* (Pic), have been regarded as synonymous with it.

An endeavour has been made in this paper to facilitate correct identification of these two species by redescribing them and adding descriptions of the male and female genitalia, which are reliable guides to identification. The main distinguishing characters are listed in Table I.

Examples of a third species of Bruchid that is dealt with in this paper were obtained from samples of seeds of the Bambarra groundnut (*Voandzeia subterranea* Thou.) brought to this laboratory from Ghana by Mr. D. W. Hall, Colonial Liaison Officer, and identified under the name *Bruchus vicinus* Gylh. var. *subinnotatus* Pic. As *B. vicinus* Gylh. has been shown by Southgate, Howe & Brett (1957) to be a junior synonym of *C. maculatus* (F.), it was desirable to ascertain whether the type of the variety represented the same species or not. Through the kindness of Dr. H. Sachtleben of the Deutsches Entomologisches Institut the type was examined and was found to represent a distinct species; the varietal name is accordingly raised to specific rank in the combination *Callosobruchus subinnotatus* (Pic). The species is redescribed in the present paper, and notes are given comparing it with the closely related species, *C. maculatus*, together with a Table showing the main distinguishing features (Table II).

Systematics of *C. chinensis* and *C. rhodesianus*.

The confusion which has arisen between *C. chinensis* and *C. rhodesianus* could have been avoided by a proper appreciation of certain constant differences between them. Skaife (1918) deals with the "Cowpea" or "Chinese" weevil in South Africa under the name *Bruchus chinensis* Thunberg, but his description and figures show clearly that he was dealing with *C. rhodesianus*. This mistake, also made by other authors, probably accounts for a number of mis-identifications of Bruchids from cowpeas (*Vigna unguiculata*) in South Africa.

As a result of examining samples of cowpeas and a large number of mounted specimens, it is the opinion of the author that *C. rhodesianus* replaces *C. chinensis* in the southern part of Africa, possibly because the former species breeds more successfully under the conditions prevailing there.

The confusion mentioned above arose from the species' descriptions being based almost entirely on the colour pattern formed by the pronotal and elytral pubescence. Linnaeus' (1758) original diagnosis of *Curculio chinensis* is exceptional, in that it records the pectinate antennae. In 1767, Linnaeus described

B. pecticornis, but later recognised it as the same species previously described as *chinensis*, and in 1790 he added *B. rufus* Deg. to the synonymy. Gemminger & Harold (1873) included *B. chinensis* Thunberg, *B. elegans* Sturm and *B. ornatus* Boh. as synonymous with *chinensis* L., and Harold (1878) added *B. adustus* Motsch. Pic (1913) repeated this synonymy, except for *ornatus*, and added *B. scutellaris*; and Decelle (1951) added *B.* (*Callosobruchus*) *rhodesianus* and *B.* (*C.*) *marshalli* Pic. Altogether eleven names have been synonymised with *C. chinensis*; notes on these are given below.

1. *pecticornis* Linnaeus, 1767. The type specimen is in the collection of the Linnaean Society of London and has been examined by the author. It agrees with the original description but it represents *Callosobruchus chinensis* (L.).

2. *rufus* De Geer, 1775. Through the kindness of Dr. Malaise of the Naturhistoriska Riksmuseum, Stockholm, the type specimen has been examined and found to be conspecific with *C. chinensis* (L.).

3. *scutellaris* Fabricius, 1792. One of the two females that form the type series was examined by the author when investigating the synonymy of *C. maculatus*; it represents *C. chinensis* (L.).

4. *chinensis* Thunberg, 1816. Gemminger & Harold (1873) and Pic (1913) list this under *chinensis* L., but Bridwell (in Larson & Fisher, 1938) synonymised it with *maculatus* F. It was shown by Southgate, Howe & Brett (1957) to belong to the genus *Bruchidius* and a new name was assigned to it, although this was later realised to be unnecessary (Southgate, 1958). The correct name is *Bruchidius chinensis* (Thunberg).

5. *elegans* Sturm, 1826, is a name that appeared in a catalogue. There was no reference to a description, nor is the whereabouts of any specimen known; it must be treated as a *nomen nudum*.

6. *ornatus* Boheman, 1829. This was shown (Southgate, Howe & Brett, 1957) to be a synonym of *C. maculatus*.

7. *adustus* Motschoulsky, 1874. Harold (1878) synonymised this with *chinensis* (L.), but it is impossible to reach a conclusion as to its status, because the original description is very inadequate and the type specimen is not available for examination.

8. *rhodesianus* Pic, 1902. Examination of the cotype in the collection of the British Museum (Natural History) has shown this species to be congeneric with, but specifically distinct from *C. chinensis* (L.), and it is redescribed below.

9. *marshalli* Pic, 1902. Comparison of a cotype with a cotype of *C. rhodesianus* in the British Museum (Natural History) has shown the two to be conspecific.

10. *barbicornis* Fabricius, 1801. This has been shown to be synonymous with *C. chinensis* (L.) (Southgate, Howe & Brett, 1957).

11. *bistriatus* Fabricius, 1801. This has likewise been shown to be synonymous with *C. chinensis* (L.) (Southgate, Howe & Brett, 1957).

TABLE OF SYNONYMY.

Callosobruchus chinensis (L.):
Curculio chinensis L., 1758
Bruchus pecticornis L., 1767
Bruchus rufus Deg., 1775
Bruchus scutellaris F., 1792
Bruchus barbicornis F., 1801
Bruchus bistriatus F., 1801

Callosobruchus rhodesianus (Pic).
Bruchus (*Callosobruchus*) *rhodesianus* Pic, 1902
Bruchus (*Callosobruchus*) *marshalli* Pic, 1902

Descriptions of Species.

Callosobruchus chinensis (L.) (Pl. XXIV, fig. 1). Antenna, inserted at mouth of emargination of eye, 4th to the apical segment, pectinate to very strongly pectinate in *male* (fig. 1, A), serrate in *female* (fig. 1, B); wholly testaceous, or with segments 4–11 dark fuscous to black. *Head* dark brown to black, confusedly punctate, sparsely covered with fine, golden pubescence;

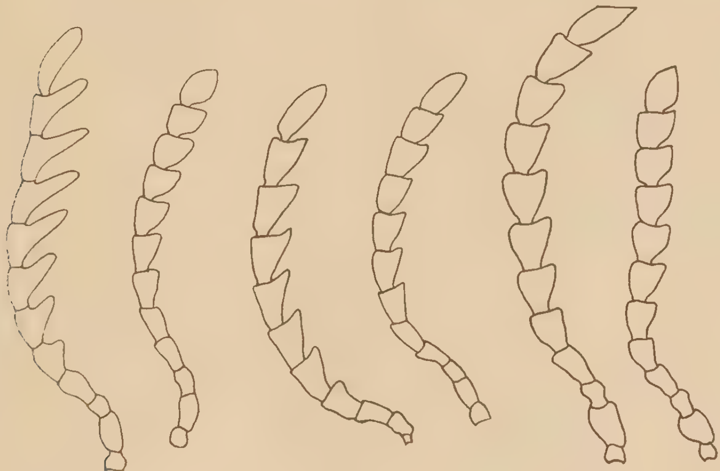

Fig. 1.—Antenna of *C. chinensis*, (A) ♂, (B) ♀; *C. rhodesianus*, (C) ♂, (D) ♀; *C. subinnotatus*, (E) ♂, (F) ♀.

median carina present, extending from basal edge of clypeus to level of posterior borders of eyes; eyes bulbous, prominent, deeply emarginate. *Thorax* conical, evenly rounded dorsally; median lobes extending well beyond basal margin; derm testaceous to black, confusedly punctate; pubescence consisting of white, golden and black setae in poorly defined patches on dorsal surface, and of white scale-like setae completely obscuring derm on median lobes. *Scutellum* black or dark testaceous, covered with white pubescence. *Elytra* together slightly longer than broad, striate, striae punctate, punctures produced on apical side to form a slight tail (Pl. XXV, fig. 1); humeral callosities prominent; derm mainly testaceous with bases and apices usually with a dark medio-lateral spot or band; pubescence on darker parts of elytra dark coloured, elsewhere golden yellow, except for white setae between and outlining dark, medio-lateral areas. *Pygidium* with sides arcuate, derm dark-testaceous to black, pubescence white, scale-like, completely obscuring derm. *Legs* testaceous, hind femur bicarinate ventrally, with a denticle situated on each carina near apex, outer tooth blunt, inner tooth long and straight, rounded at tip (fig. 2, A, B).

Callosobruchus rhodesianus (Pic) (Pl. XXIV, fig. 2). Antenna strongly serrate in *male* (fig. 1, C), serrate in *female* (fig. 1, D); wholly testaceous or with apical margins of segments 4–11 dark. *Head* reddish testaceous to black, confusedly punctate between eyes, punctures overlain with fine, golden pubescence; eyes bulbous, prominent, emarginate. *Thorax* conical, with a median, longitudinal gibbosity extending posteriorly onto and including median lobes; derm testaceous

to black, strongly and confusedly punctate; pubescence consisting of mainly golden, scale-like setae, but dark parts of derm mostly covered with dark pubescence, and white pubescence usually confined to median lobes, which are completely covered with white scale-like setae and bordered with golden setae. *Scutellum* black, covered with white, scale-like pubescence. *Elytra* (Pl. XXV, fig. 2) together slightly longer than broad; striate, striae punctate, punctures shallow and widely spaced; humeral callosities prominent; derm wholly testaceous

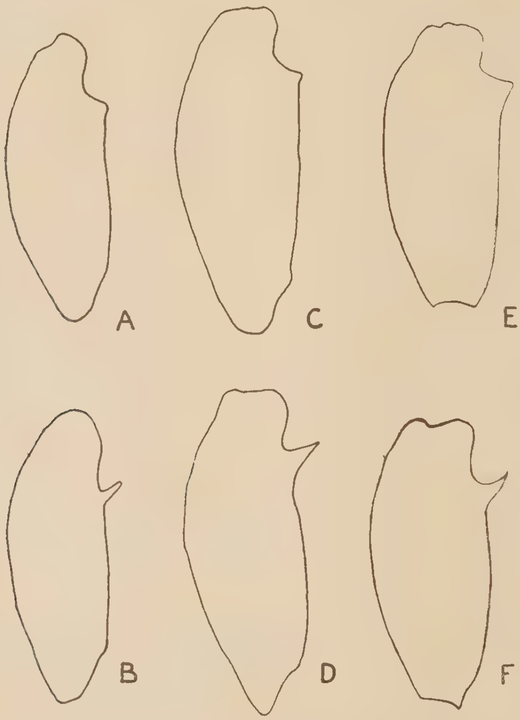

Fig. 2.—Hind femur of *C. chinensis*, (A) outer side, (B) inner side; *C. rhodesianus*, (C) outer side, (D) inner side; *C. subinnotatus*, (E) outer side, (F) inner side.

in the *male*, or with dark patches on interstices making up darker medio-lateral areas, in some examples a darker basal area extending laterally from scutellum as far as humeral callosities, pubescence of golden scale-like setae with darker setae over dark parts of derm; derm of elytron in *female* black at base and with either black apical half or dark medio-lateral area and black margins, pubescence of golden setae over testaceous parts of derm, with occasional patches of white setae, and of dark setae over dark parts of derm, except for an irregular band of white setae extending across middle of apical half of elytron. *Pygidium* with sides arcuate, acuminate apically; in *male*, derm testaceous covered with white scale-like setae; in *female*, derm fuscous, pubescence mainly fawn, scale-like, with a median, longitudinal line of white setae which may or may not extend to apex, and a small semi-circular sub-apical black spot on each side against lateral borders. *Legs* testaceous, hind pair darker; hind femur bicarinate ventrally with outer tooth blunt and inner tooth acute, curving towards apex of femur (fig. 2,

C, D); hind femur in *male* with a darker basiventral area of variable extent; in *female* with basal ⅔rds black and a black patch on basal third of hind tibia, elsewhere dark fuscous.

Callosobruchus subinnotatus (Pic).
Male (Pl. XXIV, fig. 3) derm fuscous, covered with dull white, scale-like setae interspersed with golden ones. *Head* with eyes large, bulbous, prominent, coarsely facetted, deeply emarginate; median carina present but not prominent. Antenna (fig. 1, E) twice as long as thorax, inserted at anterior edge of eye emargination, sub-serrate, three basal segments reddish testaceous, the rest wholly black or partly black with reddish-testaceous margins, apical segment elongate and narrower than sub-apical one. *Thorax* conical, evenly convex transversely, sides slightly sinuate, median lobes not prominent and extended slightly beyond posterior margin; surface confusedly punctate. *Scutellum* with white, scale-like setae only. *Elytra* (Pl. XXV, fig. 3) together 1·2 times as long as broad; striate, striae not extending to apex of elytron, striae 4, 5 and 10 shorter than the rest; humeral callosity prominent, striae 7, 8 and 9 not extending to callosity, striae 2–5 each impressed at base of elytron so that the latter appears between them as a slight ridge; striae punctate, punctures each with a slight, shallow tail. *Pygidium* nearly vertical, sides arcuate. *Legs* reddish testaceous, hind femur bicarinate, a large acute tooth present on inner carina, tooth of outer carina slightly smaller and blunt (fig. 2, E, F).
Female (Pl. XXIV, fig. 4). Derm dark fuscous to black, with whitish setae forming a pattern on the elytra. *Head* as in male, but with eyes slightly less prominent, more finely facetted and more widely emarginate. Antenna (fig. 1, F) as in male but less serrate, apical segment less elongate and as broad as sub-apical one. *Thorax* as in male, but with pubescence of dull white, scale-like setae concentrated around the median lobes and in other patches, and golden setae. *Scutellum* densely covered with a dull white pubescence. *Elytron* as in male, but pubescence mainly of golden setae, with white setae defining the sutural, basal and apical edges of a dark medio-lateral patch. *Pygidium* oblique, sides more arcuate than in male, pubescence mostly of golden setae, but with a median line of white, scale-like setae. *Legs* as in male, but sometimes darker.

Description of the Genitalia.

The terminology used in these descriptions is that adopted by Mukerji & Chatterjee (1951). The male genitalia of *C. chinensis* and *C. rhodesianus* are elongate structures, differing from those of *C. subinnotatus* and *C. maculatus*, which are much shorter and broader (Southgate, Howe & Brett. 1957). The aedeagus of *C. rhodesianus* is always very lightly chitinised and consequently very difficult to dissect from the abdomen without damage.

Callosobruchus chinensis.
Male (fig. 3, A). Parameres straight (*c*), each slightly spatulate at the apex, which is more strongly chitinised; apex rounded but asymmetrical, bearing about 15 setae, with a short apical tubercle surmounted by two or three setae; inner side of paramere with area approximately one-quarter of its length covered with extremely fine setae. Median lobe from hypomere to base of exophallic valve five-and-a-half times as long as broad. Exophallus weakly chitinised, surmounted by a spear-shaped valve bearing two longitudinal rows each of three setae (*a*). Exophallus widened below the valve giving the appearance of a collar. Within collar and situated immediately below exophallic orifice is a strongly chitinised area covered with long, narrow, apically projecting denticles. Denticulate area pear-shaped, broadest near base, narrowed anteriorly and posteriorly, usually acutely angled apically, obtusely rounded basally (*b*). Endophallus lined with

small denticles which extend over approximately basal half excluding saccus. Two strongly chitinised plates present in saccus region (d); these may be situated anterior to the lateral arches in slide-mounted specimens.

Female. The bursa copulatrix is sub-conical and composed of extremely thin chitin, so that it is almost invisible on a slide mount, except when viewed with dark ground illumination. The surface consists of a series of invaginations which may vary according to the state of the mounted specimen. In old, dried specimens the bursa may have disintegrated.

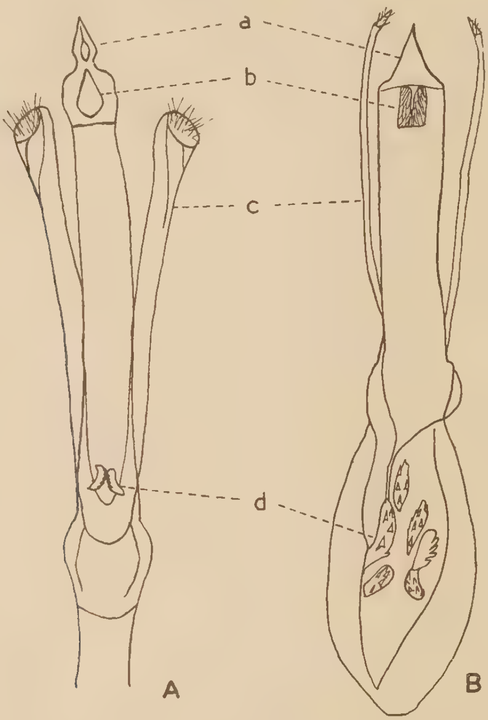

Fig. 3.—Diagramatic drawing of male aedeagus of (A) *C. chinensis*, (B) *C. rhodesianus*.

Callosobruchus rhodesianus.

Male (fig. 3, B). Parameres (c) extremely weakly chitinised for basal $\frac{2}{3}$rds, more strongly so in apical third; slightly widened towards apex, which is obliquely truncate, flattened, and bears about nine setae. Median lobe approximately three times as long as broad, consisting of the exophallus enclosing the endophallus, both being weakly chitinised. Endophallus without denticulate armature. Endophallic valve (a) triangular, bearing two setae, one on either side of midline, midway between the base and apex. Chitinised area immediately below the exophallic valve elongate, rectangular, anterior border very deeply emarginate, emargination almost reaching base; denticles on chitinised area arise from lateral and basal borders and point obliquely towards apex (b). Six chitinised plates present in saccus region, arranged in pairs and armed with strong denticles (d). Lateral arches weakly chitinised although well defined.

Female. The bursa copulatrix is less conical than in *C. chinensis*, with sides almost parallel for ⅔rds of its length and then converging towards the apex, which is almost truncate; approximately halfway along its length, on opposite sides, are two oval chitinised areas, which in some specimens are reduced to oval rings of chitin. The remaining surface of the bursa is smooth except for a few small reticulations which seem to be related to the condition of the specimen under examination.

TABLE I.

Comparison of the important distinguishing features of *C. chinensis* and *C. rhodesianus*.

Character	*C. chinensis*	*C. rhodesianus*
Antenna of male	Pectinate to strongly pectinate	Strongly serrate
Hind femur	Inner tooth long, parallel sided and at right angles to the longitudinal axis of femur	Inner tooth acute, curving towards apex of femur
Male genitalia :		
Parameres	Slightly spatulate, rounded apex bearing 15 setae	Very slightly spatulate, obliquely truncate apex bearing 9 setae
Median lobe	Length 5½ × breadth	Length 3 × breadth
Exophallic valve	Spear shaped	Triangular
Chitinised area below exophallic orifice	Deeply emarginate anteriorly	Not emarginate
Saccus region	With two chitinised plates	With six chitinised plates

Callosobruchus subinnotatus (Pl. XXV, fig. 4).

Male. Parameres almost straight, extending slightly beyond tip of the exophallic valve, apices of parameres spatulate, bearing a number of setae. Chitinised area at tip of endophallus rectangular or nearly so. Endophallic armature arranged in a mass in the hypomeral region. Two oval, chitinised plates armed with denticles present in the saccus region, sometimes obscured by the endophallic armature. Exophallic valve surmounted by a triangular tip which bears a number of setae.

TABLE II.

Comparison of the important distinguishing features of *C. subinnotatus* and *C. maculatus*.

Character	*C. subinnotatus*	*C. maculatus*
Length	4·5–5·5 mm.	2·5–3·5 mm.
Male :		
Thorax	Sides slightly sinuate	Sides evenly curved
Elytral striae*	Narrow in proportion to interstices	Broad in proportion to interstices
Pygidium	Ground colour fuscous; pubescence mainly white with interspersed golden setae	Ground colour black, or testaceous with margins and a vertical median line black ; pubescence grey or fawn
Hind femur	Inner tooth slightly longer than outer tooth	Inner tooth smaller than outer tooth
Genitalia	Apical margin of paramere truncate ; median lobe with denticles aggregated into a mass	Apical margin of paramere evenly rounded ; median lobe with denticles appearing as two columns
Female :		
Thorax	Small areas of white pubescence over parts of thorax	Golden pubescence covering whole of thorax
Legs	Dark testaceous to black	Light testaceous but with an occasional dark form
Genitalia	Bursa with triangular chitinised plate	Bursa with oval chitinised plate surmounted with denticles

* Best seen in slide-mounted material.

Female. Bursa copulatrix consists of a pear-shaped bag with two circular plates on either side of the neck, between which is a small, simple triangular structure, which is not readily visible in all specimens on account of its small size.

Summary.

The Cowpea Weevil, *Callosobruchus chinensis* (L.), has been distributed by commerce and now breeds throughout most of the tropics and sub-tropics, although in the southern part of Africa it is replaced by *C. rhodesianus* (Pic). The systematics of both species are discussed and redescriptions given of them and of *C. subinnotatus* (Pic), formerly regarded as a variety of *Bruchus vicinus* Gylh., together with an account of the genitalia of both sexes, and Tables distinguishing the first two species from one another and the third from the closely related species, *C. maculatus* (F.).

Acknowledgements.

The author wishes to express his thanks to the Commonwealth Institute of Entomology for the help given by their staff, especially Mr. R. D. Pope, who has given very valuable assistance with the manuscript. Thanks are also due to the Trustees of the British Museum (Natural History) for permission to examine specimens in their collections, and to Prof. Hans Sachtleben of the Deutsches Entomologisches Institut and Dr. R. Malaise of the Naturhistoriska Riksmuseum, Stockholm, for the loan of specimens. The photographs in this paper were prepared by Mr. J. H. Hammond. This work forms part of the research programme of the Department of Scientific & Industrial Research.

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FIG. 1. *Callosobruchus chinensis*, ♂

FIG. 2. *Callosobruchus rhodesianus*, ♂

FIG. 3. *Callosobruchus subinnotatus*, ♂

FIG. 4. *Callosobruchus subinnotatus*, ♀.

FIG. 1. *Callosobruchus chinensis,* elytron.

FIG. 2. *Callosobruchus rhodesianus,* elytron.

FIG. 3. *Callosobruchus subinnotatus,* elytron.

FIG. 4. *Callosobruchus subinnotatus,* male genitalia.

THE EFFECT OF LIZARDS ON THE BIOLOGICAL CONTROL OF SCALE INSECTS IN BERMUDA.

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Following the establishment and rapid multiplication of the scale insects, *Carulaspis minima* (Targ.) (previously recorded as *C. visci* (Schr.)) and *Lepidosaphes newsteadi* (Šulc), on the "Bermuda cedar", *Juniperus bermudiana*, which occurred in about 1941, an extended and intensive campaign of biological control was carried out against these pests. During the course of this a very large number of Coccinellids of some 25 different species was introduced into Bermuda under conditions which appeared to be ideal for their establishment. However, very few species became established, and of these only *Lindorus lophanthae* (Blaisd.) and *Microweisia suturalis* (Schwarz) developed large populations, and both diminished in numbers after being temporarily abundant. These introductions were unable to control the scales, and the virtual elimination of the cedars has resulted.

Some species of Coccinellids bred readily in Bermuda in sleeve cages on *Juniperus* branches but, as soon as the protective cages were removed, the beetles disappeared rapidly and failed to become established.

Later, a number of species of ladybirds was liberated against *Pseudaulacaspis pentagona* (Targ.) and *Pulvinaria psidii* Mask. on oleander (*Nerium oleander*). The same thing occurred, the liberated adults soon disappeared and there was no establishment even though conditions appeared to be very favourable. In 1955, an intensive study was started on the biological control of these scales, and, although several species of Coccinellids were successfully established, none developed a population sufficient to control either scale. The failure of these apparently suitable species of Coccinellids was therefore investigated.

In early 1955, a large number of adults of *Cryptolaemus montrouzieri* Muls. was liberated at Horse Shoe Bay on an oleander hedge very heavily attacked by *P. psidii*. The adult beetles were seen feeding on the scale and some larvae of *Cryptolaemus* were seen later on these bushes. However, the number of these larvae was small and the destruction of scale closely confined to a small area around the point of liberation.

It seemed possible that predators might have removed the adult beetles fairly rapidly after liberation, but that a few had laid eggs prior to their death, and that larvae from these were developing successfully on the scales. In the subsequent generation the number of larvae was still further reduced and from then on no example of *Cryptolaemus* was seen, even though abundant host material was still available.

Observations were made in a number of areas, and it seemed possible that insectivorous birds and lizards might be responsible for the disappearance of the Coccinellids. Insectivorous birds are uncommon in Bermuda and it seemed most unlikely that they could have caused the disappearance of the Coccinellids; on the other hand, lizards are very abundant everywhere.

Predation by Lizards (*Anolis* spp.).

An experiment was therefore carried out in October 1955 at Frank's Bay where 1,000 adults of *Cryptolaemus* were liberated on an isolated oleander tree

TABLE I.

Results of dissections of *Anolis grahami* in Bermuda, September–October 1956.

(S = small lizard, M = medium-sized lizard, L = large lizard.)

Type of prey	Area where lizard caught									
	Frank's Bay 3L 5M 3S	Frank's Bay (2) 1L 1M 1S	Cluster Cottage 3L 4M 1S	Chanticleer 5L 14M 19S	Roxdene 3L 2M 3S	Rocklands 2M 2S	Miscellaneous 1L 3M 4S	Salt Kettle 3L 1M 2S	St. George's 2M	Total 19L 34M 35S 88
	Nos. of prey									
COCCINELLIDAE:										
Azya	—	—	—	3	2	—	—	—	—	5
Cryptolaemus ..	2	—	—	—	—	—	1	—	—	3
Scymnus (*Diomus*)	2	—	10	4	—	6	2	—	—	24
Lindorus	—	—	38	—	—	1	7	—	—	46
,, larvae ..	—	—	11	—	—	—	—	—	—	11
Scymnus (*Pullus*)	—	—	2	26	1	—	—	—	—	29
Larvae (*A.* & *C.*)	40	3	1(*A*)	8(*A*)	—	—	2(*A*)	—	—	54
NITIDULIDAE :										
Cybocephalus ..	—	—	—	—	—	72	—	—	—	72
BLATTIDAE	—	—	—	1	—	—	—	1	—	2
GRYLLIDAE	—	—	—	—	—	1	—	—	—	1
PSOCIDAE	—	12	—	36	1	—	—	1	—	50
LABIDURIDAE ..	—	—	—	3	—	—	—	—	—	3
Coleoptera	4	1	6	17	4	—	—	3	—	35
Homoptera ..	3	—	—	4	—	—	—	—	—	7
Aphis	—	43	145	51	—	—	—	21	—	260
Pulvinaria ..	—	—	—	34	6	—	—	5	—	45
Pseudaulacaspis ..	—	—	—	—	—	8	—	—	2	10
Thysanoptera ..	—	—	—	—	—	—	—	—	—	—
Lepidoptera ..	7	—	5	11	13	—	3	4	2	45
,, larvae ..	8	1	7	25	3	5	1	2	2	54
Diptera	2	2	4	36	1	19	—	2	3	69
Hippelates ..	—	—	—	52	—	—	13	—	2	67
Hymenoptera :										
Iridomyrmex ..	—	—	10	158	4	—	4	17	—	193
Pheidole	5	—	—	24	—	—	109	—	37	175
Brachymyrmex ..	—	18	—	665	—	—	6	—	—	689
Sp.A. (Ant) ..	—	—	—	36	—	—	—	—	—	36
Aphytis	—	—	—	—	—	—	—	—	78	78
Microterys ..	—	—	2	5	—	—	—	1	—	8
Cheiloneurus ..	—	—	—	2	—	—	—	—	—	2
Phanerotoma ..	5	1	—	—	—	—	—	—	—	6
Apis	—	—	—	1	—	—	—	—	—	1
Chalcids	—	—	1	27	—	2	—	—	—	30
Arachnida	5	—	1	1	—	—	—	—	—	7
Mite	—	—	—	1	—	—	—	—	—	1
Wood-louse ..	—	—	—	1	—	—	—	—	—	1
Snail	—	—	—	1	—	—	—	—	—	1
Tail of lizard ..	—	—	—	1	—	—	—	—	—	1
Cast skins of lizard	—	—	—	2	2	—	1	—	—	5
Lantana fruits ..	—	5	—	—	—	—	—	—	—	5
Seed–graminaceous	—	—	—	1	—	—	—	—	—	1

heavily infested with *P. psidii*, and on which there were a number of lizards, *Anolis grahami*. Liberation was made at 3.30 p m. and immediately the lizards became active, and several examples of *Cryptolaemus* were seen to be eaten. The following morning two lizards were caught and dissected. One large one about 6 in. long had eaten 26 adults of *Cryptolaemus*, the other, a small lizard 4 in. long, had eaten two. There were about 20 lizards on this tree and it is obvious that they could have decimated the Coccinellid population in a comparatively short time.

However, in June 1956 a few examples of *Cryptolaemus* were still present on this tree, and, in addition, 100 adults of *Azya luteipes* Muls. (= *A. orbigera* Muls.) were also liberated here. At the same time an effort was made to destroy the lizards, as it was thought that recolonisation of this isolated tree by lizards might take some time. By early August, numbers of adults and larvae of both *Cryptolaemus* and *Azya* were very large and the attack of *Pulvinaria* was very obviously under control. A few lizards occurred periodically on the tree and some of these were shot and dissected (see Table I). A considerable proportion of the identifiable insects in the guts of 11 lizards were larvae of *Azya* and *Cryptolaemus*.

During this period, September–October 1956, 1,656 adults and pupae of *Azya* and *Cryptolaemus* were removed from this tree for colonisation elsewhere, and by October the infestation of *Pulvinaria* on the original tree had been eliminated, although elsewhere in Bermuda attacks of *Pulvinaria* had been building up during this time.

Anolis grahami is common all over Bermuda. It was introduced in 1905 in an attempt to control the fruit-fly, *Ceratitis capitata* (Wied.). Recently a second species, *Anolis leachi*, has been introduced into Bermuda. It is much larger than *A. grahami* and is gradually spreading out from Warwick and West Paget where apparently it was originally introduced. In these areas it appears to be replacing *A. grahami* to a certain extent. Where it occurs there are only very few individuals of the latter species and these are small.

Dissections of Lizards.

Since it appeared that the lizards might be an important factor in the survival of Coccinellids and hence in the biological control of scales in general, it was decided to make a survey to determine exactly what they were eating. During September and October 1956, 88 examples of *Anolis grahami* were shot (see Table I) and dissected. In addition, 9 specimens of *A. leachi* were dissected (Table III). During January a further 88 (quite fortuitously) of *A. grahami* and 37 of *A. leachi* were examined in order to determine if there were any great seasonal differences in their diet (Tables II and IV). These lizards were classified approximately according to size and any identifiable insects in the guts were listed. The results in Tables I–IV show all the insects identifiable either whole or from parts. Naturally, this is not an exact list of all that these lizards had eaten, since much of their food, particularly in the hind parts of the gut, was so macerated as to be unidentifiable. It is likely, therefore, that although these Tables give a fairly accurate general idea of what the lizards were eating, there are several factors which probably produce quantitative errors. Fragile and entirely soft-bodied insects are likely to be rendered unidentifiable in the gut more quickly than harder-bodied species. Certainly species such as Coccinellids, which were being specially sought, were identifiable more readily from small fragments than others. However, within these limits, the results of the dissections are most interesting. It should be pointed out that all lizards dissected were shot on oleander trees bearing attacks of scales, and in most instances in areas where *Azya* or *Cryptolaemus* had been liberated. No lizards were taken from areas

TABLE II.

Results of dissections of *Anolis grahami* in Bermuda, January 1957.

(S = small lizard, M = medium-sized lizard, L = large lizard.)

Type of prey	Area where lizard caught										
	Loughlands 8L 17M 11S	Burnt House 2L 2M	Banjo Island 3L 3M 5S	Cluster Cottage 2L	Devon Vale 1L 1M 1S	Coral Beach 4L 3M	Rocklands 1L 1M	Chanticleer 1M 2S	Miscellaneous 1L 4M	Chelston 8L 7M	Total 30L 39M 19S / 88
	Nos. of prey										
COCCINELLIDAE :											
Azya	3	—	—	—	—	—	—	—	—	4	7
,, larvae ..	55	—	—	1	—	—	—	—	—	1	57
Scymnus (*Diomus*)	1	—	—	—	—	—	—	—	—	—	1
Lindorus ..	7	7	—	—	—	—	—	—	—	4	18
,, larvae	—	—	—	—	—	—	—	—	—	1	1
Clitostethus ..	—	—	—	—	—	—	—	—	—	1	1
Cybocephalus ..	—	1	—	—	—	—	—	—	—	—	1
Cryptognatha ..	1	—	—	—	—	—	—	—	—	—	1
BLATTIDAE :											
Periplaneta spp.	—	—	1	—	—	2	—	—	—	1	4
TETTIGONIIDAE ..	—	—	—	—	—	—	—	—	—	1	1
PSOCIDAE	—	—	—	—	—	—	—	1	—	—	1
LABIDURIDAE ..	3	—	—	—	—	—	—	—	—	—	3
Embioptera ..	—	—	—	—	—	—	—	—	—	1	1
Coleoptera ..	18	3	6	2	2	3	—	—	—	7	41
Hemiptera	7	—	2	—	—	—	1	—	2	2	14
Aphis	71	20	8	106	16	—	—	—	4	4	229
Pulvinaria ..	9	—	—	—	—	—	—	1	2	88	100
Pseudaulacaspis	1	—	—	—	—	1	—	—	1	—	3
Pseudococcus ..	14	—	2	—	—	1	1	—	3	—	21
Thysanoptera ..	4	—	—	—	—	—	—	—	1	1	6
Lepidoptera ..	7	1	5	1	1	3	—	2	2	5	27
,, larvae	3	1	6	1	1	—	—	2	1	—	15
Diptera	49	10	33	2	4	8	7	4	8	29	154
Hymenoptera :											
Iridomyrmex ..	133	5	—	9	—	63	6	5	1	38	260
Pheidole ..	—	—	88	—	131	26	—	—	137	—	382
Brachymyrmex ..	185	4	61	—	12	101	—	73	3	—	439
Aphytis	96	—	—	—	—	—	—	6	—	2	104
Microterys ..	2	—	—	—	—	—	—	—	—	—	2
Metaphycus ..	—	—	—	—	—	—	—	—	—	1	1
Ichneumonoidea	9	1	—	—	—	1	—	2	1	1	15
Chalcidoidea ..	27	—	2	—	4	—	—	—	—	1	34
Acarina	—	—	—	—	—	—	—	—	1	—	1
Arachnida	2	—	1	—	4	2	—	1	2	3	15
ONISCIDAE	—	—	—	—	2	—	—	—	—	1	3
Myriapoda	2	—	—	—	—	—	—	—	—	—	2
Centipede ..	—	—	1	—	—	—	—	—	—	—	1
Lizard	1	—	1	—	—	—	—	—	—	—	2
Cast skins of lizard	3	—	2	—	—	—	—	—	—	1	6

such as *Citrus* orchards, for example, where fruit-flies might be expected to occur, but the general diet of the lizards is likely to be similar in all localities.

It was hoped, by liberating different species of Coccinellids obtained from Trinidad, and examining the gut contents of lizards shot near the liberation points at different times after the liberations, to obtain some idea of the length of time that food took to pass through the alimentary canal, and from this to obtain a better quantitative measure of the numbers of insects, and particularly Coccinellids, being eaten in a given period of time.

This experiment was disappointing, as only a single such Coccinellid (an individual of *Cryptognatha simillima* Sic.) was obtained from dissection and no conclusion could be drawn.

In the autumn dissections there were found, in the 88 examples of *Anolis grahami*, 2,110 individual insects distinguishable, together with seven Arachnids, five cast lizard skins, five *Lantana* fruits, one grass seed, a mite, a wood-louse, a small snail and a lizard tail. In addition, there were several small stones.

TABLE III.

Results of dissections of *Anolis leachi* in Bermuda, September–October 1956.

Number of lizards dissected = 9 (4 large, 2 medium-sized and 3 small).

Type of prey	Nos. of prey
COCCINELLIDAE :	
Lindorus	6
Azya larvae ..	1
BLATTIDAE	4
Coleoptera	5
Homoptera	1
Pseudaulacaspis ..	4 females
Thysanoptera.. ..	1
Lepidoptera ..	5
,, larvae ..	6 (+ 2 eggs!)
Diptera	1
Hymenoptera :	
Iridomyrmex ..	10
Arachnida	2

Of the insects, 244 were Coccinellids (and *Cybocephalus* sp.) or their larvae, 1,093 ants, 260 Aphids, 55 scales, 99 Lepidopterous adults or larvae and 124 parasitic Hymenoptera. Of the Coleoptera, a fair proportion were of *Leptostylus praemorsus* (F.), a species which bores into twigs of oleander and *Citrus*.

In the January dissections, comparable figures were 1,944 insects distinguishable in the 88 examples of *A. grahami* together with 15 Arachnids, one Acarine, six cast skins, two small lizards, three wood-lice, one centipede and two millipedes. Of the insects, 87 were adults or larvae of Coccinellids and *Cybocephalus*, 1,081 ants, 229 Aphids, 103 scales, 42 Lepidopterous adults or larvae, and 156 parasitic Hymenoptera.

These figures show striking similarities, and the figures from the two groups of dissections have therefore been divided, very arbitrarily, into three groups according to whether they are in general harmful, beneficial or neutral. These are shown in Table V. There are several interesting points, although this is naturally a very broad classification with a number of obvious errors; for example, all Diptera are not harmful, the predacious Cecidomyiids are beneficial, a number of the Coleoptera are neutral, and a number of the Aphids were already parasitised.

Discussion on Results of Dissections.

It is to be noted that the total number of insects found in the same number of specimens of *Anolis grahami* was very similar during the two periods. This is somewhat surprising as in the colder weather the lizards are very much less active, and are only so during the warmer periods of sunny days. On dull, cold days they remain sheltering in débris at the base of trees, in holes in stone walls, etc. Being poikilothermic animals their general rate of metabolism is correlated with the temperature of the environment and it would have seemed probable that the metabolic rate, and hence food consumption, would have been less during the colder weather.

TABLE IV.

Results of dissections of *Anolis leachi* in Bermuda, January 1957.

(S = small lizard, M = medium-sized lizard, L = large lizard.)

Type of prey	Area where lizard caught: Rocklands 3L 3M 6S	Cluster Cottage 1L 1S	Burnt House Hill 8L 10M 5S	Total 12L 13M 12S — 37
	Nos. of prey			
COCCINELLIDAE :				
Scymnus (*Diomus*) ..	—	—	2	2
Lindorus	2	9	27	38
,, larvae	—	2	1	3
Clitostethus	—	—	5	5
Cybocephalus	—	—	1	1
BLATTIDAE :				
Periplaneta spp. ..	8	—	19	27
TETTIGONIIDAE	2	—	3	5
PSOCIDAE	1	—	—	1
LABIDURIDAE	1	—	1	2
Coleoptera	13	2	13	28
Hemiptera	—	—	3	3
Aphis	1	—	—	1
Pulvinaria	—	1	4	5
Pseudaulacaspis	1	—	—	1
Pseudococcus	1	—	—	1
Thysanoptera	1	1	—	2
Lepidoptera	6	—	12	18
,, larvae	5	5	7	17
,, pupae ..	2	—	—	2
Diptera	128	1	14	143
Hippelates	68	—	—	68
Hymenoptera :				
Iridomyrmex	41	11	86	138
Brachymyrmex	5	—	—	5
Apis	—	—	1	1
Ichneumonoidea	3	—	6	9
Chalcidoidea	3	—	—	3
ONISCIDAE	—	3	2	5
Myriapoda	—	—	3	3
Cast skins of lizard ..	1	—	1	2
Seed	—	—	2	2

There is also a general similarity in the numbers of the various orders taken by the lizards. There are a few definite differences; the number of Coccinellids is lower in January, correlated presumably with a noticeable reduction in the numbers seen in the field. The same is true of *Cybocephalus*. Psocids were well represented in August but not in January, Lepidoptera and their larvae were less common in January, but the numbers of the rest of the groups are remarkably similar in the two periods.

TABLE V.

Food of *Anolis grahami*, according to Orders and Families, grouped roughly into beneficial, neutral and harmful species.

	September-October 1956	January 1957
Beneficial species		
Coccinellidae	172	86
Cybocephalus	72	1
Hymenoptera–Parasitica ..	124	156
,, Apoidea	1	—
	369	243
Neutral species		
Blattidae	2	4
Psocidae	50	1
Labiduridae	3	3
Embioptera	—	1
	55	9
Harmful species		
Thysanoptera	1	6
Gryllidae & Tettigoniidae ..	1	1
Coleoptera	35	41
Hemiptera	322	367
Lepidoptera	99	42
Diptera	136	154
Hymenoptera–Formicidae ..	1171	1081
	1765	1692

The fact that there is a preponderance of harmful species is not necessarily of great significance. In both cases about two-thirds of this total is due to worker ants which do not represent breeding units, and their destruction as individuals is not equivalent, in its effect on their populations, to that of the destruction of other insects (with the exception of the one honey bee). A number of the Lepidopterous larvae were, in fact, parasitised.

Of the neutral species the rôle of cockroaches has been shown (Simmonds, 1955) to be beneficial with regard to their feeding on *Pseudaulacaspis pentagona*; bearing this in mind, and also their generally accepted noxious status, they were classed as neutral.

From their effect on the populations of *Pulvinaria* and *Pseudaulacaspis* the most important groups are the Coccinellids (and *Cybocephalus*) and the Hymenopterous parasites, of which over two-thirds of those encountered were parasites of the two scales. It is obvious that the effect of lizards on these groups is considerable, particularly on the Coccinellids (and *Cybocephalus*), which are not

particularly common, and which moreover as predators can destroy large numbers of scales during their development and adult life. Lizards, therefore, undoubtedly have a considerable effect in the biological control of these scales.

This general picture of the prey consumed by lizards gives rather a false impression of their habits, in so far that the food consumed by individuals may be very different from the average and, as is shown below, some individual lizards may feed on a limited range of species during some periods, in spite of the fact that all the lizards came from the same type of environment (see p. 603). The gut contents naturally vary very considerably from lizard to lizard; there were no marked differences observable between males and females or between lizards of different sizes except in so far that a very small lizard could not eat a very large insect. When sloughing their skins, lizards were found to have very little in their guts, and it would seem to be normal that a sloughed skin is eaten after it is shed.

From a consideration of each dissection, some examples of which are given below (pp. 608–609) it was obvious that some individuals tend to concentrate, for short periods at least, on a single or few species of prey whilst others take a more varied diet. This has been found to be true with bird predators, which in some cases tend to feed exclusively on a common food species, ignoring for a time any other food. For example, starlings, *Sturnus vulgaris* (which were shot on a freshly ploughed field), dissected in 1940 in Norfolk, England, were found to contain nothing but Tipulid larvae which were abundant in the field, other insects, *e.g.*, wireworms (Elaterid larvae), having been ignored. Kirkpatrick (1925) studied the food of the buff-backed egret, *Bubulcus ibis* (cited as *Ardea ibis*), in Egypt, and the results from his dissections show remarkable similarities to those obtained in the present dissections in so far that some of the individual birds tended to concentrate on single species of prey, often species which would appear very small for a bird of this size, *e.g.*, *Syrphus corollae* F., *Corixa* sp.; others, as with the lizards, were more general feeders. It seems likely that the individual predator may become sensitive to the " pattern " produced by one particular food species on its senses and reacts more often and more quickly to that pattern. In the same way, entomologists searching for a particular type of insect develop an " eye " for it, ignoring other species to a large extent.

There are many examples of this in these dissections. One lizard from Roxburgh House contained one Lepidopterous larva and 105 workers of *Pheidole megacephala* (F.). Three lizards from the Frank's Bay " experimental " tree contained (1) four larvae of *Cryptolaemus*, (2) one adult and one larva of *Cryptolaemus*, and (3) 19 larvae of *Azya* and *Cryptolaemus*. These lizards were feeding exclusively on Coccinellids. Another from the same area contained 10 Coccinellid larvae, one adult of *Cryptolaemus*, two spiders, a beetle, a moth and a moth larva.

An individual from Rocklands contained an immature cricket, a large and a small Lepidopterous larva, two large flies, one Hymenopterous parasite, six adults of *Scymnus* (*Diomus*) *thoracicus* (F.), and 14 of *Cybocephalus*.

A small individual from Chanticleer had eaten a small moth larva and 16 workers of *Iridomyrmex humilis* (Mayr), another large lizard contained two large flies, two adults of *Hippelates pusio* Lw., eight workers of *Iridomyrmex*, one beetle and 20 Psocids; another, four black Chalcids and 23 workers of *Brachymyrmex* sp.

A lizard from Cluster Cottage had eaten 13 adults and 11 larvae of *Lindorus lophanthae* along with two small flies, two workers of *Iridomyrmex*, and a small moth.

Another large lizard contained 43 examples of *Aphis gossypii* Glov. together with 5 fruits of *Lantana camara*; a lizard from Chanticleer had 25 workers of *Brachymyrmex* only in it, another 93 workers of *Brachymyrmex* and three adults of *Scymnus thoracicus*. A large specimen from Cluster Cottage had consumed

74 examples of *A. gossypii* (some of them parasitised) along with 12 other insects. One large lizard from St. George's, where a heavy attack of *Pseudaulacaspis* had built up, contained 78 adults of *Aphytis ?diaspidis* (How.).

One large lizard from Palm Grove contained 137 workers of *Iridomyrmex* and nothing else, one from Loughlands had 67 workers of *Brachymyrmex* amongst the 87 insects in its gut, another had 34 workers of *Brachymyrmex* out of a total of 48 insects, another had taken 71 examples of *Aphis gossypii* out of a total of 86 insects.

One remarkable feature was the fact that even large lizards took a large number of insects which would have been considered too small as prey on grounds of size. One medium-sized lizard from Loughlands had eaten 23 examples of *Aphytis* along with one large and one medium-sized fly, two Aphids, three small beetles and four examples of *Lindorus*.

At Chelston, in Paget, several of the lizards dissected had fed on *Pulvinaria*, 11 lizards containing, amongst their prey, 0, 0, 0, 0, 0, 0, 1, 8, 10, 23, 24 full-grown examples of *Pulvinaria*, respectively. Thus several of the lizards here had developed, at least at this time, a taste for the scales themselves, a feature only observed in this one area.

Many other examples of certain species of insects being selectively eaten by these individuals of *Anolis* could be given, but the above is sufficient to indicate the tendency. Although this selective feeding is often directed towards species which are particularly common in the lizard's habitat, this is not always so. With the Coccinellids and *Cybocephalus*, which naturally have been particularly studied, *Anolis grahami* has specialised on *Azya*, *Cryptolaemus* (and their larvae), *Scymnus* spp. and *Cybocephalus* when these have been plentiful in an oleander tree, but have also apparently developed a taste for larvae of *Lindorus* and *Azya* when these have not been particularly common. In January, 56 adults and four larvae of *Lindorus* were found in the guts of the specimens of *A. grahami* and *A. leachi* dissected, but none was seen alive in the field. Thus this preference for a single species or group of species is not necessarily only for a particularly common insect, although abundance may affect the selection. All lizards in one area do not necessarily select the same or similar prey. Thus, at Loughlands, while some contained a high proportion of *Azya* larvae, one contained nothing but workers of *Iridomyrmex* and some had eaten adults of *Aphytis* in some numbers.

The dissections of *Anolis leachi* give, *mutatis mutandis*, similar results and conclusions (see Tables III & IV). Although, in January, 38 examples of *Lindorus* were found in 37 specimens of *A. leachi*, this species appears to be more partial to cockroaches (27), grasshoppers (5) and large Lepidopterous larvae (17) than does *A. grahami*, probably on account of its very much larger size. Even so, a considerable number (143) of workers of *Iridomyrmex* was taken. As with *A. grahami*, some individuals of this species seem to feed intensively on a few or even one species of prey (*e.g.*, *Iridomyrmex*) which would be thought to be unsuitable on account of size or possibly of unpalatability. One specimen of *A. leachi* had eaten 68 examples of *Hippelates*, a very small species for the size of the lizard. They also ate more ONISCIDAE than did *A. grahami*.

A. leachi is at present restricted in distribution but is spreading, and its effect on the populations of Coccinellids is likely to be similar to that of *A. grahami*.

The results of these dissections are somewhat surprising. It might have been assumed that the larger and more succulent insects would be more suitable for food for the lizards, and it is certainly surprising that small ants, Psocids and minute parasitic Hymenoptera are eaten, often almost exclusively by some individuals, both large and small. This together with the small amount of food in the guts of some non-moulting specimens, and the fact that *Lantana*, *Juniperus*,

one unknown seed and one grass seed were also eaten (the latter perhaps accidentally on seizing an insect for food), rather indicates that, in general, food may be scarce for the lizards, or competition keen. It has always been assumed that Coccinellids are distasteful to predators; both adults and larvae exude a fluid when attacked, the adults often show "warning coloration" and some of the larvae, including those of *Azya* and *Cryptolacmus*, have protective waxy coverings.

It is possible, therefore, that at present in Bermuda, owing to its abundance, *Anolis grahami* (and to a certain extent *A. leachi*) is short of food and is not very selective in the food eaten, except in so far as individuals become used to attacking a single species of prey.

It is possible, too, that if the numbers of lizards were reduced, the food supply, even if at the present level, would be relatively more adequate, and that the species could be more selective in its prey. If this were so, it is also possible that Coccinellids might to a certain extent be avoided.

Naturally this will have to have experimental confirmation.

Experiments in Control of the Lizards.

Apart from cats around houses, there are no predators of *Anolis* in Bermuda and the lizards can and have reproduced unchecked. If an effective predator could be introduced and the numbers of lizards reduced, the result might be an increase in the numbers of Coccinellids and the possibility that other species of ladybirds could be introduced, with a consequent increased control of scales; and it is even possible that adequate control of *Juniperus* scales might be achieved and allow recolonisation by the Bermuda cedars.

This is of course speculative, but it is worth trying to eliminate the lizards on an experimental scale. Two methods of doing this are being tried. A direct attempt is being made to exterminate *Anolis* on a selected island, Banjo Island in St. George's, and consideration is being given to the biological control of the lizards.

Direct control.

Banjo Island has had all the débris and much of the vegetation cleared from it, leaving the oleanders, which have had dead wood, etc., cleaned away from their roots. To date, some 300 examples of *A. grahami* (*A. leachi* is absent here) have been shot in the four months to January 1957. The island is about two-third of an acre in area. Assuming, as seems reasonable, that with regard to the population of *A. grahami* it is typical of the whole of Bermuda, which covers about 12,000 acres, then the population of *A. grahami* in Bermuda is of the order of 5,000,000.

Both *Pulvinaria* and *Pseudaulacaspis* have now been established on Banjo Island and, in the near future, liberations of Coccinellids will be made to determine the interaction of the populations of the predators and scales in the absence of lizards.

Biological control.

The second experiment involves the introduction of some predator that will attack the lizards, but which will not, it is hoped, be undesirable in any other way. For instance, predacious snakes might be successful but are unsuitable since Bermuda has no snakes, and they might detract from the tourist attractions of the island.

A number of birds have been suggested in connection with this but various considerations make them unsuitable. The Australian kookaburra, *Dacelo gigas*, was at first thought suitable but was ruled out on account of its raucous, and

often nocturnal, cries and the fact that it may eat small birds. *Halycon malimbicus* and *H. senegalensis* from West Africa and *H. smyrnensis* from India and Ceylon, all "kingfishers" which in fact eat lizards, snails, crabs, etc., have been considered, but the difference in climate and lack of suitable nesting sites in Bermuda would probably prevent establishment, even if the birds could be brought alive to Bermuda, and they are difficult species to transport. However, if possible, it is likely that these will be tried.

A further possibility, and that considered by several authorities to be the most promising, is that of the kiskadee, *Pitangus sulphuratus*, which occurs in Trinidad. This species feeds on large insects and also eats lizards. It perches on a vantage point on a tree, pole or the like, and pounces down on its prey seen in the open spaces below. It is found commonly around houses and in comparatively built-up areas, and in this respect would be suitable for Bermuda. It nests in high trees, and with the loss of the cedars this may be a difficulty in Bermuda. Trial shipments of these birds have already been made. Shipments were started in December 1956 since, although it was realised that the climate of Bermuda was most unfavourable at this time, it was hoped that they would breed during the ensuing spring. Birds were collected on "bird-lime" in Trinidad and placed in a cage 6′ × 6′ × 6′ with an adequate perch. Insects were placed in this for food but no great interest was shown and many of the birds died. Since it was found at this time impossible to keep birds successfully in cages for more than a day or two, they were shipped to Bermuda as soon as possible after they were caught. Six birds were placed in a lightly constructed cage 24″ × 14″ × 12″ and they were shipped by air express, the transit time being about 10 hours. The majority of birds died in transit, but, particularly with the last shipments, 9 and 10 out of 12 birds in each consignment arrived alive, but obviously in a weakened condition. In the last shipment these were released in a storage house at the Aquarium in Bermuda and provided with water. As they arrived at dusk a light was left on so that during the night they could feed on cockroaches, which were abundant. However, in the morning only three were alive. These were liberated but have never been seen, and it must be presumed that they have died. It seems that all have succumbed to a combination of maltreatment after collection, lack of food prior to shipment, probably fright, and starvation during the flight and subsequent night, and inclement weather in Bermuda.

Birds are now being acclimatised to artificial food, of which minced beef appears to be best, and it is hoped that mortality in future shipments will be less.

It is, of course, uncertain what the actual effect of these birds would be if well established in Bermuda, but if there are any undesirable effects—for example, an increase in house-flies or *Hippelates*, which seems unlikely—it would be quite possible in an area the size of Bermuda and with birds as large and spectacular as these to eliminate them if necessary.

If on the other hand a noticeable reduction in the lizard population occurred, the food supply for the remainder might be improved and the Coccinellids, supposedly distasteful, might be neglected to a certain extent. This would result in an increase in the population of Coccinellids and a subsequent decrease in the attacks by scale insects. This would obviously take a comparatively long time to achieve.

Summary.

In an intensive study, begun in 1955, on the biological control of *Pseudaulacaspis pentagona* (Targ.) and *Pulvinaria psidii* Mask. on oleander (*Nerium oleander*) in Bermuda, several species of COCCINELLIDAE were successfully established, but none developed a population sufficient to control either scale. The

failure of these apparently suitable species of Coccinellids was therefore investigated. It seemed possible that insectivorous lizards, which are very abundant everywhere, might be responsible.

Dissection of a number of lizards, *Anolis grahami*, and *A. leachi*, in the autumn and winter indicated that at both these times their effect on the natural enemies of scale insects in general and of *Pseudaulacaspis pentagona* and *Pulvinaria psidii* in particular, was considerable. Both Coccinellids and Hymenopterous parasites were eaten in large numbers. A surprising number of very small insects, including ants, was eaten, and although a number of the insects eaten are harmful, on balance it would appear that, particularly with regard to the biological control of scale insects, the elimination from Bermuda of these lizards, which are introduced species, would be beneficial.

Experiments are being carried out to test this, and the introduction of predacious birds, particularly that of the Trinidad kiskadee, *Pitangus sulphuratus*, is planned.

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MOVEMENTS OF THE VECTORS OF VIRUS DISEASES OF CACAO IN GHANA.

I.—CANOPY MOVEMENT IN AND BETWEEN TREES.

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Contents.

It has been shown (Cornwell, 1956) that the practice of felling and piling virus-infected cacao trees is an efficient method of preventing vectors from spreading infection to healthy cacao. Nevertheless, the removal of more than 60 million infected trees in Ghana since swollen-shoot disease was first recorded in 1936 has not completely halted virus spread, and over ten million diseased trees continue to be felled annually. Incomplete control may be attributed to delay in starting a cutting-out campaign on an adequate scale and to interruptions after its initiation. Because of these factors the number of diseased trees has become so enormous that, in spite of the present rate of progress, large numbers must perforce remain, for some time to come, a continuing source of infection. This applies particularly to the Eastern Province, although the position elsewhere, notably in Ashanti, is encouraging. Furthermore, control operations have not included the treatment of latently infected contact trees in addition to those which show symptoms, and three species of forest tree, *Cola chlamydantha*, *Ceiba pentandra* and *Adansonia digitata* (Posnette, Robertson & Todd, 1950; Dale & Attafuah, 1957) have been shown to be naturally infected in the field. After treatment, therefore, reservoirs of the virus remain for the further spread of infection to healthy cacao. The rate of spread is aggravated by the close planting of farmers' cacao and monoculture of the crop over vast areas. Present knowledge of spread is largely based on observations of the development of infections in the field and on limited studies of vector movements. Detailed investigations on the rate of movement, multiplication and distribution of the virus within the tree have not been made.

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Observations on the development of cacao-virus outbreaks indicate that two distinct types of spread occur: (1) radial spread from the edges of established outbreaks, and (2) "jump spread" with the formation of new infections at varying distances from existing outbreaks, sometimes in otherwise disease-free areas. Frequently, outbreaks when found consist of a localised scatter of diseased trees, or groups of diseased trees are delimited by small zones of healthy ones. In very few cases, however, is it possible to attribute with certainty the infection of a particular tree to one or other of these types of spread, particularly in areas of "mass infection" where many outbreaks are coalescing. A further complication is the presence of latently infected trees, which make it difficult to assess the extent and direction of virus spread at any time.

There is evidence that movement of the mealybug vectors of cacao viruses may take place across the ground (Strickland, 1951*a*; Cornwell, 1956), and by wind currents (Strickland, 1950). Strickland (1951*a*) has also suggested that movement may take place from tree to tree *via* the canopy branches. Whilst it has been shown that terrestrial movement is of limited extent (Cornwell, *op. cit.*) the significance of the other two methods of vector dispersal has not been previously assessed. The present work details experiments carried out to investigate canopy movement of the dominant vector, *Pseudococcus njalensis* Laing, and to determine the importance of this movement in relation to the spread of cacao virus. A second paper reports investigations into aerial movement of the vectors.

Methods.

Populations of vectors moving on cacao trees were sampled by attaching to the trees pieces of fresh cacao twig upon which the mealybugs rested to feed. The twigs were collected on the day required from selected trees, cut to a standard length of eight inches, and fumigated in a hydrogen cyanide chamber. They were then pinned in pairs at marked positions on the trunks and branches of the experimental trees. In most cases scaffolding was erected to allow access to branches which could not be reached from the ground. The twigs were exposed for periods not exceeding 24 hours, removed with as little disturbance as possible and examined in the field under a binocular microscope. Those which were exposed for longer periods soon wilted and became unpalatable to mealybugs. Various numbers of paired twigs were used in the experiments described below. Attempts were made to assess the ratio of the total surface area of the twigs to that of the experimental trees, but these estimates were considered unreliable for the calculation of absolute numbers of mobile insects. Identification of the instars of *P. njalensis* was carried out as described previously (Cornwell, *op. cit.*) by microscopical examination and measurement of the hind tibio-tarsi.

The Movement of Mealybugs on Individual Trees.

The first experiment was carried out to investigate movement on trees supporting feeding populations of 2,000–3,000 mealybugs. The trees were about 20 ft. high, growing under forest shade in conditions typical of peasant cultivation. Branches which touched neighbouring trees were pruned to isolate the mealybug populations.

Composition and size of the mobile population.

Twelve pairs of bait twigs were used to sample populations on each of six trees. They were attached to the trunk at one ft. above the ground, and at two-ft. intervals up the trunks and along the canopy branches. Pairs of twigs were duplicated in the canopy at 13–17 ft. All were examined and replaced by fresh pieces on 87 days between the beginning of April and end of July 1955. A

total of 953 mealybugs was recorded. The uniform composition of the mobile populations on the six trees is shown in Table I; 92 per cent. of mealybugs were first-instar nymphs and less than 2 per cent. were adults. The numbers of insects recorded from day to day varied between 0 and 58, less than 10 being caught on 61 days and more than 20 on ten days. A maximum daily catch of 33 mealybugs

TABLE I.

Composition of the mobile population of *P. njalensis* on cacao.

Instar \ Tree	1	2	3	4	5	6	Total	%
I	47	269	154	79	79	247	875	91·8
II	8	12	7	4	4	11	46	4·8
III	1	4	2	2	1	7	17	1·8
Adult	3	2	0	6	1	3	15	1·6

was recorded on a single tree. Of the 15 adults recorded, two were being carried in the mouths of ants (*Crematogaster striatula* Emery), which had not been disturbed. There is no evidence to suggest that bait twigs are more palatable to mealybugs than the experimental trees themselves and, as the surface area of these twigs is exceedingly small in relation to the total area of the trees, the results indicate that, during 24 hours, many hundreds of vectors may be actively moving on heavily-infested cacao.

TABLE II.

Numbers of mealybugs caught on paired bait twigs at different heights on six cacao trees.

	Trunk					← First jorquette →	Canopy		
Height (ft.)	1	3	5	7	9	11	13	15	17
Trees 1	0	1	6	6	3	12	3, 9	3, 7	4, 5
2	10	43	7	14	13	15	18, 45	29, 41	3, 49
3	1	2	3	8	42	40	9, 17	14, 23	1, 3
4	3	0	3	6	5	11	5, 11	11, 14	9, 13
5	1	4	15	12	9	5	4, 12	9, 9	0, 5
6	26	33	11	17	13	3	16, 25	20, 35	29, 40
Total log (n + 1) mealybugs	3·67	4·65	5·23	6·20	6·31	6·38	13·12	14·30	10·70
Mean (n) mealybugs per site per tree	3·1	5·0	6·4	9·7	10·2	10·5	11·3	14·5	6·8
% distribution	4·0	6·4	8·3	12·5	13·2	13·6	14·7	18·7	8·8

Distribution of the mobile population.

The percentage distribution of mobile mealybugs on the trunks and branches is shown in Table II. Because of an extreme variation in the numbers caught at the different levels, a log (n + 1) transformation of the data has been employed. Table II shows that there is a linear increase in catch from the base of the tree up to a height of 15 ft., followed by a decrease at 17 ft. Density of mobile mealybugs is influenced by the structural arrangement of the trunk and branches of cacao; those walking down the branches move on to the trunk at the first jorquette, resulting in a localised increase in density at this point. Density below the jorquette is influenced by the extent to which vectors continue moving downwards and whether or not they leave the tree at ground level. Conversely, mealybugs walking up the branches become less dense when moving towards the outer canopy. In a later section, evidence is provided which indicates that the distribution at the various levels is also influenced to some extent by the temperature difference between ground level and the top of the canopy. The present results show that the numbers caught in the middle canopy are more than four times greater than those recorded at the one-ft. level. This figure may be compared with Strickland's data (1951*a*), which shows that 87 per cent. of feeding mealybugs are distributed in the canopy.

The percentage distribution shown in Table II is based on the mean number of insects caught on each pair of twigs and provides an index of mealybug density at the sites of the traps. To examine the distribution of mobile insects on a whole tree, these indices must be integrated with respect to the number of branches and surface area of the bark at the different heights. Because such measurements are difficult to make, and inaccuracies will affect strongly the proportions of insects at the different levels, the distribution on a whole tree has not been assessed.

Factors influencing mealybug movement.

Earlier work (Cornwell, 1956) showed that under the most unfavourable conditions for mealybug survival, when infested cacao wood is cut and subject to prolonged wilting, adults tend to remain at their feeding sites and frequently die there. In the present work, the low numbers of adult mealybugs recorded on bait twigs confirms the opinion that the mature insect is essentially non-mobile. This behaviour on the living tree results in the formation and growth of colonies which persist, enclosed in carton tents constructed by attendant ants, at a particular site for many months.

Changes in the mobile population of mealybugs on cacao are brought about by reproduction or death of the static population and by changes in environmental factors which influence mobility. It has been shown (Cornwell, 1957*a*) that there are rapid and frequent changes in total population, brought about by predation and parasitism by natural enemies. There is no period during the year when populations remain virtually unchanged for more than a few weeks. Since adults of *P. njalensis* are ovo-viviparous and eggs may hatch to produce mobile first-instar nymphs in less than 45 minutes (Strickland, 1951*a*), no attempt has been made in the following experiments to distinguish between the effects of environmental factors on the rate of reproduction and on individual mobility.

To determine the conditions which influence the numbers of mobile insects, four environmental factors were measured. Temperatures were recorded at 9 a.m. and 3 p.m. in a Stevenson screen about half a mile from the experimental area. Using Cambridge continuous-recording thermometers, air temperatures were recorded in the experimental trees at the top of the canopy and at ground level. Bark temperatures were measured with a mercury thermometer sealed into a cacao trunk with paraffin wax. The number of hours of sunlight was also recorded. Light intensity was measured in arbitrary units with a

photographic exposure meter, readings being taken from four sides of white-painted trays having sides sloping at an angle of 45 degrees. The trays were placed under the cacao canopy and in a clearing a few yards from the experimental trees. Changes in saturation deficit were recorded by measuring changes in evaporation from Livingstone atmometers placed six ft. above ground, under the cacao canopy.

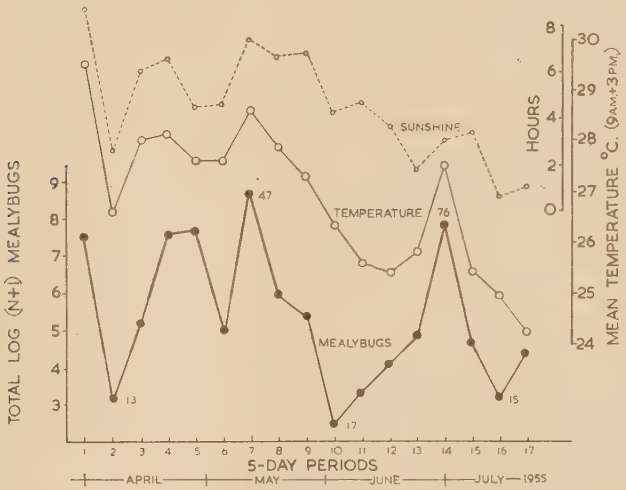

Fig. 1.—Changes in the numbers of mobile mealybugs on cacao during 17 weekly 5-day periods between 29th March and 23rd July. The position of each numbered period is that of its middle day. Changes in mean temperature and hours of sunshine are positively correlated with changes in catch.

The numbers of mobile mealybugs recorded on four cacao trees between April and July are shown in fig. 1, together with changes in the mean temperature (9 a.m. + 3 p.m.) and number of hours of sunshine. Bait twigs were examined daily and catches for each tree were transformed to log (n + 1) and summed for 5-day periods. The total log (n + 1) catch is shown as the ordinate, whilst maximal and minimal arithmetic totals are shown in the body of the graph. A regression analysis between temperature and catch provided a significant correlation coefficient ($P < 0{\cdot}001$) of $+0{\cdot}73$. A further analysis between hours of sunlight and catch provided a less significant correlation coefficient ($P < 0{\cdot}05$) of $+0{\cdot}57$. Of the two environmental factors, the effects of which are inseparable, it would appear that temperature is the more important in influencing numbers of mobile mealybugs. Changes in evaporation showed no significant correlation ($r = +0{\cdot}23$) with catch over a period of 12 weeks.

To reduce changes in catch resulting from changes in tree infestation, a more critical experiment was carried out over a shorter period. Twigs were attached at selected positions to one heavily infested tree during July and August 1955. An examination was made of changes in the number of mealybugs moving throughout the day by attaching and replacing bait twigs seven times between 7 a.m. and 6.30 p.m.; twigs were exposed in sequence for $1\frac{1}{2}$ hrs. during $2\frac{1}{2}$-hr. sampling periods. This routine was carried out on 14 days and a total catch of 174 bugs and a daily range of 6 to 25 insects was obtained. From the measurements taken with continuous-recording thermometers, a mean temperature

TABLE III.

Catches of mobile mealybugs during the day, compared with the mean of temperatures recorded at ground level and at the top of the canopy. Solid and dotted lines indicate the 23·5°C. and 24·5°C. "isotherms", respectively.

Date / Sampling periods (hr.)	07·00–09·30	08·30–11·00	10·00–12·30	11·30–14·00	13·00–15·30	14·30–17·00	16·00–18·30	07·00–09·30	08·30–11·00	10·00–12·30	11·30–14·00	13·00–15·30	14·30–17·00	16·00–18·30
	Numbers of mealybugs							Mean temperature (°C.)						
26.vii	1	0	0	2	3	2	0	21·9	22·8	23·3	23·9	24·3	24·1	23·9
28.vii	0	0	1	1	4	3	0	22·1	22·8	23·1	24·0	24·6	24·1	23·2
30.vii	0	0	0	3	3	5	0	21·7	22·3	22·8	23·4	23·8	23·6	22·7
3.viii	0	1	0	2	1	3	1	22·7	23·7	23·9	24·1	24·5	24·6	24·4
5.viii	1	0	0	2	1	0	2	21·1	21·8	22·5	23·3	24·7	25·0	24·5
9.viii	0	2	1	3	1	5	2	21·7	22·5	23·5	24·4	24·7	24·6	23·9
11.viii	0	0	1	3	5	3	0	22·2	23·0	23·8	24·4	24·7	24·7	23·7
17.viii	1	0	1	6	4	1	0	21·5	22·7	23·8	24·8	25·6	25·6	24·6
20.viii	1	0	2	5	4	1	2	21·5	23·0	24·2	25·1	25·4	25·2	24·6
23.viii	0	0	1	0	2	2	1	22·2	23·2	23·8	24·4	24·8	24·5	23·8
25.viii	1	0	0	4	6	8	0	22·3	23·1	23·7	24·5	25·2	25·3	24·0
27.viii	0	0	1	6	11	4	3	22·6	24·0	24·9	26·0	26·4	26·3	25·7
30.viii	0	1	1	5	5	3	2	22·4	23·6	24·6	25·5	25·9	25·8	24·7
31.viii	0	1	0	1	5	2	2	22·5	23·2	23·6	24·0	24·5	24·4	23·6
Total log (n + 1)	1·50	1·38	2·58	7·80	8·95	7·65	3·60	Mean						
% distribution of n	2·7	2·5	5·1	25·2	32·4	24·3	7·8	22·0	23·0	23·7	24·4	24·9	24·8	24·1

(11 a.m. to 4 p.m.) was calculated. A regression analysis between this mean and the daily catch (totalled log (n + 1) catch for all trapping sites) provided the significant correlation coefficient ($P < 0{\cdot}001$) of $+0{\cdot}83$ (fig. 2). On comparing the catch with the mean 9.0 a.m. and 3.0 p.m. temperature recorded in the screen, a positive correlation ($r = +0{\cdot}66$, $P < 0{\cdot}01$) was also obtained. An attempt to correlate the catch with the screen temperature of the day prior to

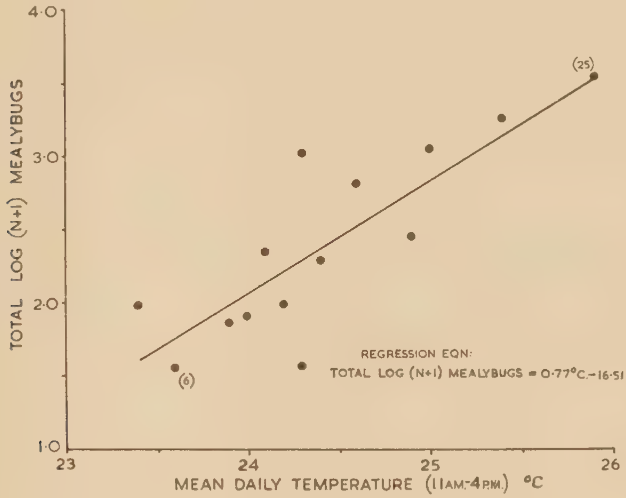

Fig. 2.—Relationship between the daily catch of mobile mealybugs and the mean daily temperature. Maximal and minimal arithmetic totals are shown.

trapping provided a correlation coefficient ($+0{\cdot}07$) which approximates to zero, indicating the absence of a 24-hour delay in response to temperature. When examining the relationship between the daily catch and number of hours of sunlight, a non-significant correlation ($r = +0{\cdot}45$) was obtained.

Changes in the number of mobile mealybugs during the day are shown in Table III. There is very little activity during the morning; movement is initiated about noon and the numbers of mobile vectors increase markedly to reach a maximum at about 3 p.m. There is a decrease in activity between 3 and 6 p.m. Changes in air temperature followed a similar pattern on all days during which trapping was carried out, rising to a maximum towards mid-afternoon and falling towards sunset. A regression analysis between the mean temperature and log (n + 1) catch for the 98 trapping periods provided the significant correlation coefficient ($P < 0{\cdot}001$) of $+0{\cdot}66$, indicating an immediate response to prevailing temperature. This result would suggest that the number of vectors moving is an index of individual mobility rather than of reproduction rate. By determining the appropriate regression equation (log (n + 1) bugs = 0·167°C. – 3·64) it was shown that movement is initiated at about 23·5°C. The 23·5°C. "isotherm" embraces 92 per cent. of the total catch, whilst the 24·5°C. "isotherm" embraces 66 per cent. (Table III).

Temperatures in the canopy rise more rapidly and reach higher maxima than at ground level (fig. 3) indicating that conditions in the canopy are more conducive to the maximum number of insects moving than at levels below the canopy. This suggestion is substantiated by data from the earlier experiments, which show that on good trapping days (when more than 10 mealybugs were caught), 59 per

cent. of the catches were recorded at or above 13 ft.; on poor trapping days (when less than 10 insects were caught), this figure was reduced to 45 per cent. The bark temperature on the trunk reaches a lower maximum than the air temperature (fig. 3), the greatest difference between these temperatures occurring towards mid-day. Changes in light intensity are erratic, but corresponding variations were recorded in the clearing and under the cacao canopy. These variations are caused

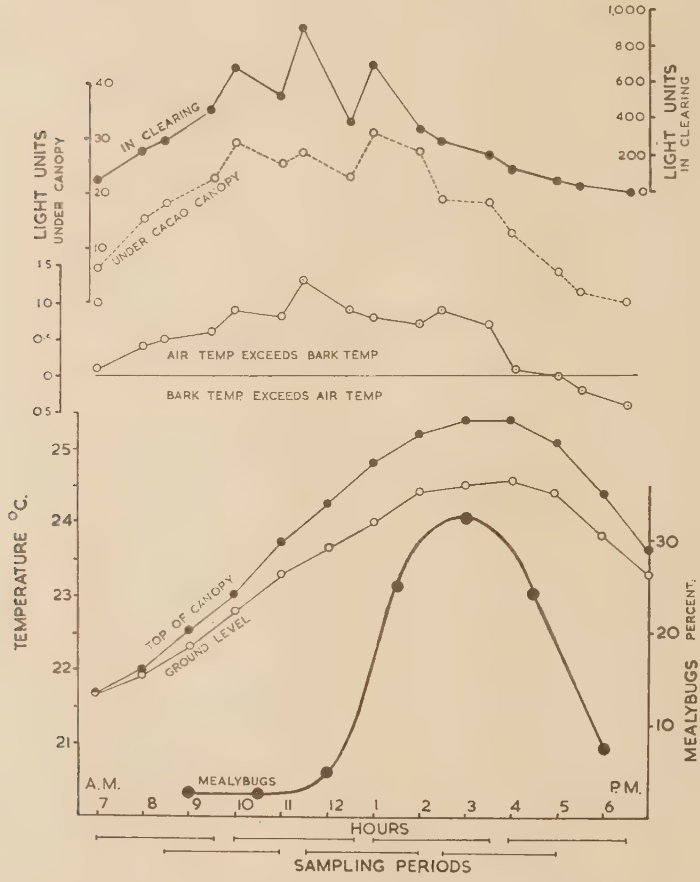

Fig. 3.—Changes in the abundance of mobile mealybugs during the day. Changes in air temperature at the top of the canopy (19 ft.) and at ground level are shown, together with differences between air and bark temperatures at 8 ft. Changes in light intensity in a clearing and under the cacao canopy show similar fluctuations. All data are means for 14 days.

largely by the obstructing influence of the giant forest trees. Maximum light intensity was recorded at 11.30 a.m. when the sun is vertically overhead and influence of the forest trees is at a minimum; there is penetration of direct sunlight on to the cacao canopy and this is associated with a rise in temperature. It will be noted that the time of maximum insolation coincides with the initiation of mealybug movement.

The Movement of Mealybugs between Trees.

In a further series of experiments, an examination was made of the extent to which mealybugs move *via* the canopy branches from one tree to the next. Obviously, such movement can only occur when the branches of neighbouring trees are in contact. In Ghana, this is nearly always so; in fact an interlocking canopy is a characteristic feature of cacao cultivation. A closed canopy is believed to be essential for good yielding, it provides a safeguard against the species of MIRIDAE that attack cacao (Williams, 1953; Taylor, 1954), and suppresses competing weeds. The degree of interlocking depends on the age and spacing of the trees. The first experiment was carried out to establish that, under normal conditions of cacao cultivation, mealybug movement from tree to tree can occur. Data were then collected on the effect of spacing on the growth of cacao trees of known age. Finally an examination was made of mealybug movement under artificial conditions and studies were made on trees grown at various spacings.

Movement of radioactive mealybugs in farmers' cacao.

In a previous communication (Cornwell, 1956) studies of mealybug dispersal were made using insects labelled with tracer levels of radioactive phosphorus. Cacao seedlings infested with mealybugs were grown in nutrient culture solution containing ^{32}P and the insects were released in the field. Using radiation detection equipment the direction and rate of travel of the vectors could be studied despite their small size. Furthermore, the experimental insects could be distinguished with certainty from all others in the field. It was initially considered that this technique could be best applied to the present study by the radioactivation of whole cacao trees, thus labelling the vectors at their feeding sites on the canopy branches. Experiments showed, however, that such labelling for ecological studies was difficult to effect because of inefficient uptake and localised translocation of the active material by mature trees (Cornwell, 1957*b*). Thus, in the present study, mealybug-infested radioactive seedlings (grown in nutrient culture solution containing ^{32}P at a concentration of 20 mc./litre) were again employed, these being tied to the canopy branches of a mature tree.

The tree selected had an extensive canopy, 15–20 ft. above the ground, in contact with the canopies of three adjacent trees. The trunks of the four trees were thickly smeared with banding grease a few inches above the ground. A total of about 4,000 labelled mealybugs infested the radioactive seedlings when these were fixed in position at two or three ft. from the ends of the terminal branches of the release tree. Fifteen pairs of cacao twigs were also attached to the branches of this tree and 30 pairs to each of the three contact trees. During the following fortnight, 58 mealybugs were caught, of which 25 were radioactive; 19 labelled insects were recorded on the release tree, and 2, 4 and 0 on the three contact trees. The radioactive insects provided a mean counting rate of 255 c.p.m. The results of this experiment established, without doubt, that mealybugs are able to walk from tree to tree *via* the canopies of cacao grown under peasant cultivation.

The effect of spacing on the growth of cacao.

In Ghana, farmers' cacao is grown at a mean density of about 600 trees/acre, which corresponds to an average planting distance of 8½ ft. Because such cacao is planted randomly, three beans to each hole and additional beans are frequently "self-sown", trees may be found growing within a few inches of each other, and localised densities of 2,000–2,500 trees/acre are commonplace. Under these conditions, the canopies of adjacent trees are indistinguishable.

To determine the effect of spacing on the growth of eight-year-old Amelonado cacao, data were collected (in the W.A.C.R.I. "Spacing Trial", Anon., 1949) on

the maximum width of the canopy, the number of terminal branches and the number of these in contact with adjacent trees. Measurements were taken on 20 trees, randomly selected, of the spacings, which ranged from 4 to 15 ft. Maximum canopy spread was recorded along the rows in two directions at right-angles, a vertical pole being held at either side of the tree and a measuring tape run between the poles at trunk level. Branch counts had to be made without felling and large counting errors are acknowledged. Furthermore, extreme variability in the growth of cacao, even that grown on a plantation basis, contributes to the great variation in the results obtained (fig. 4).

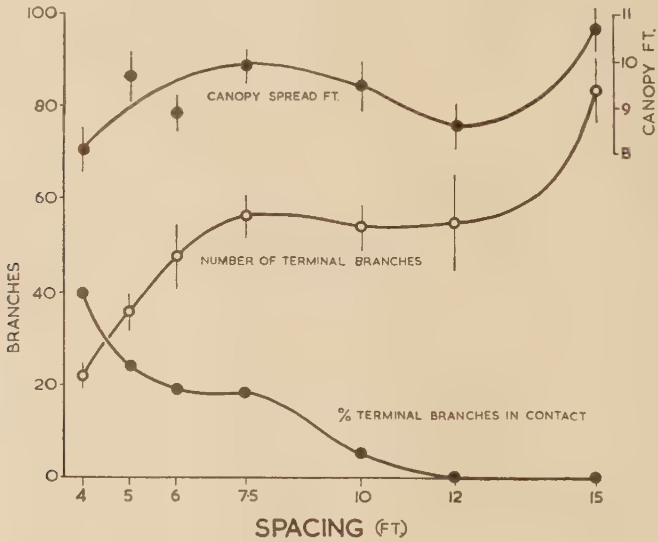

Fig. 4.—Growth characteristics of 8-year-old Amelonado cacao grown at seven spacings. Vertical lines represent standard errors of mean measurements from 20 trees.

The data show that maximum spread of the canopy varies little at the seven planting distances. There is apparently greater spread at 7½ ft. and 15 ft.; the reduction in growth of trees planted 12 ft. apart may be attributable to stunting of the branches, associated with greater insolation and attack by cacao Mirids. A recorded mean spread of 8·1 ft. at 4-ft. spacing (2,800 trees/acre) indicates that the whole width of the canopy of one tree is intermixed with branches of adjacent trees and that some branches may even touch those of the second tree in the row. The results also show that wider spacing of trees between 4 and 7½ feet apart assists in the development of terminal branches; there is no difference in the number produced at spacings of 7½, 10 and 12 ft., but considerably more are produced at 15 ft. Spacing also influences the height of the canopy. Close planting produces a canopy of which the lowest branches may be 15 ft. above the ground, whilst 12- and 15-ft. spacings may cause branches to grow and persist at waist level. Counts of the number of branches touching adjacent trees diminish from 40 per cent. at 4-ft. spacing to about 20 per cent. at 5–7½ ft. The apparently favourable conditions for growth at 7½-ft. spacing produce a plateau in the curve for the percentage of terminal branches in contact. The data show that in eight-year-old Amelonado cacao the canopies of adjacent trees are isolated at spacings greater than 12 ft. It may be concluded

that the spacing of cacao, within the range investigated, produces sufficiently marked differences in growth habit to influence strongly the rate of spread of mealybugs from one tree to the next.

Mealybug movement under artificial conditions.

To examine the capacity for movement of mealybugs walking horizontally over wood, a structure was erected to simulate plantation cacao growing in lines seven ft. apart. Twenty nine large oil drums, standing on end, were arranged as shown in fig. 5. Each drum supported a wooden board, 3-ft. square, with

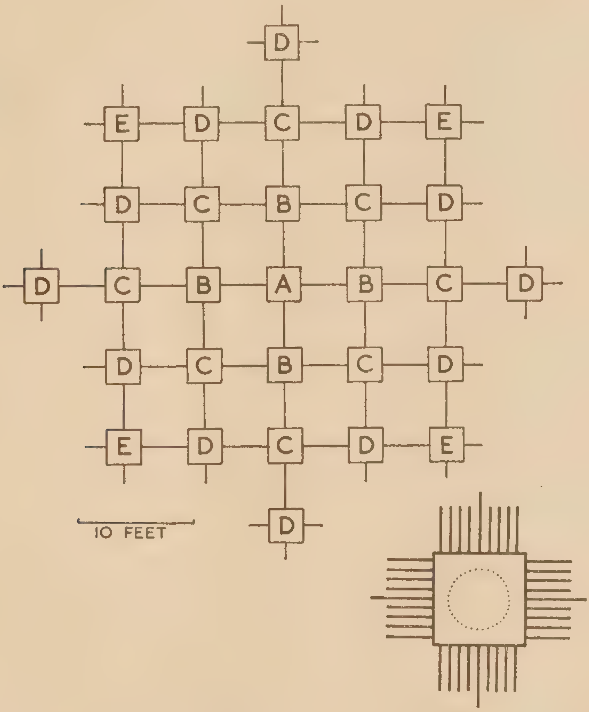

Fig. 5.—Plan diagram of a model of plantation cacao. A, release platform; B, C, D and E, rings of contact platforms. Inset shows details of platform arrangement with 36 "branches", four of which touch adjacent platforms.

36 holes drilled round the edges. Into these holes were inserted 32 pieces of wood 18 in. long and $\frac{3}{4}$ in. square in section (the "branches") and the remaining four holes, one at the centre of each side, held similar pieces of wood 4 ft. long ("branches" in contact), joining adjacent boards. A large pile of infested cacao twigs was placed on the centre platform to provide a source of mobile mealybugs; mealybugs tend to move as their host tissues wilt, 80 per cent. of such insects being first-instar nymphs (Cornwell, 1956). This arrangement was used to study the effect on mealybug movement of doubling the number of "branches" in contact from 11 per cent. in the first experiment to 22 per cent. in a repeat experiment. Movement from one platform to the next was examined by attaching one bait twig to each of the 1,044 "branches". The twigs were inspected daily and replaced by fresh pieces over a period of a fortnight. Each drum was smeared with banding grease at its base to prevent possible movement

of mealybugs across the soil, and the whole experimental area shaded by roofing with plantain leaves and palm fronds at six ft. above the ground. With 11 per cent. of " branches " in contact, a total of 2,596 mealybugs was recorded. The distribution of insects on the various platforms is shown in Table IV and fig. 6.

TABLE IV.

Dispersion of mealybugs on a model of plantation cacao.

Percentage of " branches " in contact			11%		22%	
Location	Minimum distance of movement (in ft.) measured from platform centres	No. of platforms and designation	No. of mobile mealy-bugs	Ratios of catch per platform	No. of mobile mealy-bugs	Ratios of catch per platform
Release platform	2*	1, A	2491	100	3211	100
1st ring of contacts	7	4, B	56	0·56	128	1·00
2nd ring of contacts	14	8, C	23	0·12	66	0·26
3rd ring of contacts	21	12, D	19	0·06	72	0·19
4th ring of contacts	28	4, E	7	0·07	20	0·16
Total mobile mealybugs			2596		3497	

* Since the 8-in. bait twigs lie along the " branches " their proximal ends are 2 ft. 4 in. from the centre, from which a spread of 4 in. is allowed for the pile of cacao twigs. Over the longer distances this allowance is unnecessary.

In the second experiment, with eight of the 36 " branches " per platform in contact (22%), a total catch of 3,497 mealybugs was obtained. These results show that vectors walked many feet in search of favourable feeding sites, distances of at least 28 ft. to the outermost ring of contact " trees " being covered.

Since studies of terrestrial movement (Cornwell, *op. cit.*) showed that mealybugs exhibit no marked directional orientation, it may be assumed that movement from a release point consists of random dispersion, and that the distribution of mealybugs at a particular time represents a balance of positive and negative movements with respect to the source. In studying this dispersion, it is important to recognise the limitations of the artificial arrangement shown in fig. 5; firstly, the bait twigs provide the only source of food, which may encourage wider movements than under field conditions, and secondly, dispersion on the outer platforms is restricted. Examination of fig. 5 shows that the " D " platforms at the compass points are likely to support fewer mealybugs because the latter can only reach them from one " C " platform; whereas the other " Ds " can be reached *via* two " Cs " and occasionally, perhaps, from an " E ". These limitations apply when 11 or 22 per cent. of " branches " are in contact. However, in common with field conditions, while there is only one *direct* route from " A " to " B " and to " C " and " D " at the compass points, there are two *direct* routes to other " Cs ", three to other " Ds " and six to each " E ". These differences are likely to affect the rate of dispersion at different distances from the release point.

The data have been analysed by two methods. Firstly, for each ring, the catch per platform has been expressed as a ratio of that on the release platform (100), thus providing a comparison of vector density from a standard sample of bait twigs. Secondly, a regression coefficient has been calculated (a coefficient of diffusibility, indicating the rate of change of vector density with distance) using the total catch in each ring from all bait twigs at a standard density per unit area.

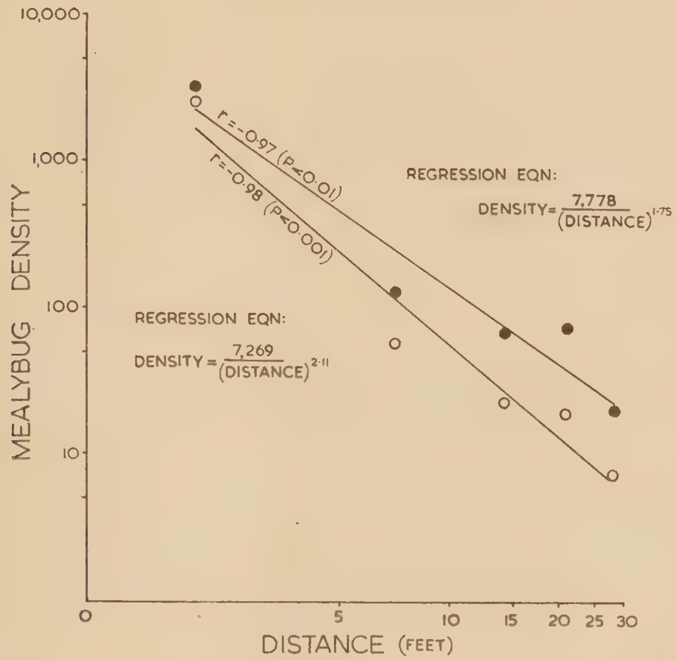

Fig. 6.—Relationships between mealybug density and distance of movement on a wooden model of plantation cacao, with 11 per cent. (open circles) and 22 per cent. (closed circles) of "branches" in contact.

With 11 and 22 per cent. of "branches" in contact, the ratios of the numbers of insects found on the "branches" of each of the first-ring platforms to those recorded on the "branches" of the release platform were only 0·56 and 1 : 100, and for those of the second ring 0·12 and 0·26 : 100. There was, therefore, a marked reduction in catch within a few feet of the release point, but, at greater distances, this reduction became much less pronounced. An explanation of this result has been given above, but it may also be attributed to the removal of mealybugs on bait twigs from the release "tree", insects which might have walked further if a suitable feeding site had not been provided. Using the first method of analysis, the results show conclusively that a doubling of the number of canopy bridges provides a comparable increase in dispersion. The second method provided regression coefficients of $-\log 2{\cdot}106$ and $-\log 1{\cdot}748$. Retransformed, these values become -128 and -56, which differ by a multiplication factor of 2·28.

Mealybug movement in plantation cacao.

The movement of mealybugs between real trees was examined on uninfested cacao growing 4, 5, 6 and 7½ ft. apart. Mealybug-infested cacao twigs and ten pairs of bait twigs were tied to branches of a central release tree, and a further ten pairs of bait twigs were attached to the terminal branches of each of eight

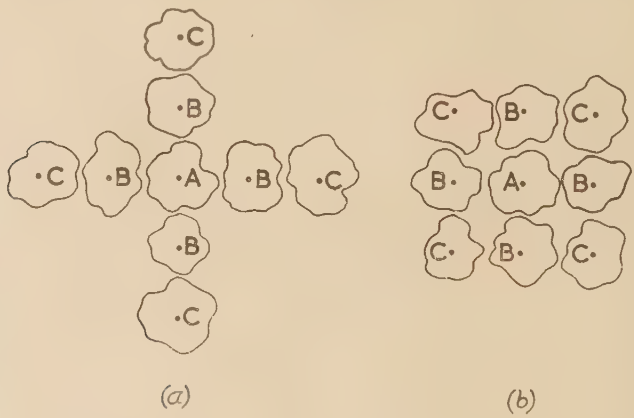

Fig. 7.—Plan diagram showing arrangement of release (A) and contact trees (B and C) in studies of mealybug movement in plantation cacao. For details of experiments (a) and (b), see text.

neighbouring trees. Trees used in the first experiment (fig. 7a) were growing 6 ft. apart, four being adjacent to the release tree and four in the second ring. In a second experiment (fig. 7b), eight trees adjacent to the release tree were used and studies were made at each of the four spacings. Trunks of the experimental trees were grease-banded. Trapping was carried out daily for two weeks.

TABLE V.

Numbers of mealybugs recorded on release and neighbouring trees growing at 4-, 5-, 6- and 7½-ft. spacings. The mean number of mealybugs per contact tree is expressed as a ratio of the catch on the release tree.

Experiment	1		2							
Spacing (ft.)	6	Ratio	4	Ratio	5	Ratio	6	Ratio	7½	Ratio
Release tree (A)	146	100	53	100	453	100	547	100	189	100
4 Contact trees (B)	9	1·54	23	8·73	18	1·16	17	0·66	17	1·72
4 Contact trees (C)	2	0·34	14		24		12		9	
Total	157		90		495		576		215	

The catches (Table V) were analysed by the first method only, since too few trees were used to allow accurate determination of regression coefficients. In the first experiment the ratio of the numbers of mealybugs found on each adjacent contact tree averaged 1·5 : 100 of those caught on the release tree and about four times those which reached each of the second four trees, this latter proportion

being similar to that obtained with the wooden model. In the second experiment, at 4-ft. spacing, large numbers of mobile insects (in a ratio averaging about 9:100 of those caught on the release tree) reached adjacent trees; at wider spacings (5 to 7½ ft.) there was a marked reduction in dispersal and only small differences in distribution between spacings were obtained, the ratios at all spacings being less than 2:100 as in the first experiment. At close spacings, branches from adjacent trees may be in contact at many points. Therefore a non-linear relationship is to be expected between the percentage of branches in contact and percentage mealybug dispersal, which would explain the more marked dispersal which occurred at 4-ft. spacing.

Discussion.

Strickland (1951*a*) stated " . . . there is little doubt that the interlocking canopy of West African cacao is ideal for the dispersal of *P. njalensis* and swollen shoot. A mealybug has only to walk perhaps half an inch to find itself on a leaf belonging to a new host tree ". Also, he suggested (1951*b*) that since adult mealybugs tend to remain static " . . . it follows that tree to tree migration is probably nymphal in character ".

The present work has shown that some of the mealybugs on cacao become mobile at temperatures exceeding 23·5°C. and that activity is maximal during mid-afternoon. The mobile population is composed almost entirely of first-instar nymphs, which increase in density from the base of the trunk to a maximum within a few feet of the top of the canopy. Experimental evidence confirms the suggestion that mealybugs move between trees *via* interlocking canopy branches. Nymphs walk over appreciable distances in search of new feeding sites and adults are occasionally carried by *Crematogaster* ants.

Because the experiments were carried out on healthy cacao the infectivity of mobile insects was not examined. In assessing the importance of canopy movement in relation to virus spread it is necessary, therefore, to consider two questions. Firstly, whether first-instar nymphs feed before leaving the colonies or during their peregrinations and, secondly, whether infective insects, which become mobile, are capable of transmitting the virus at new feeding sites. With regard to the first question, Dale (1958) has observed nymphs, 0–1 days old, on infected cacao seedlings apparently feeding, but positive transmissions were not obtained. With nymphs 1–2 and 2–3 days old, 8 and 48 per cent., respectively, transmitted the virus (New Juaben). Regarding the second, Lister (1953) has shown that starvation periods longer than 24 hours after infection feeding are required to inhibit completely transmission by first-instar nymphs. This evidence shows, therefore, that first-instar nymphs, even when no more than 2–3 days old, are efficient vectors, and there can be little doubt that, because of the short distances involved and their walking speeds of about two inches per minute (Cornwell, 1956), the time spent by mealybugs in moving between feeding sites does not seriously reduce the efficiency of virus transmission. Meteorological data recorded at Tafo indicate that temperatures are unlikely to be a limiting factor in mealybug movement. Minimum temperatures exceed 23·5°C. on about one night per year, but maximum temperatures are lower than this critical level on three or four days only. Whilst conditions are suitable for movement throughout the year, greater activity is likely to occur during the dry season, December to February, when temperatures frequently exceed 32°C.

Radial spread of swollen-shoot disease from the edges of established outbreaks has been attributed to the canopy movement of vectors between adjacent trees. The present evidence makes this assumption all the more plausible. The results have shown that the ratio between the number of mobile mealybugs that reach adjacent contact trees growing at 4-ft. spacing and the number that remain on the tree on which they originated is 9:100, though the corresponding figure is only

1 or 2:100 when the trees are 5 to 7½ ft. apart. Since large numbers of insects may be actively moving under favourable conditions, even the smaller ratio is of considerable significance, particularly as one infective insect feeding on a healthy contact tree may be sufficient to extend infection.

Prevention or reduction of this type of vector movement would involve modifications in cultural practice. There are three possible methods: (1) pruning existing cacao to isolate mealybug populations; (2) planting cacao on a plantation basis at wide spacings; and (3) retention of close spacing and provision of a barrier to infection by interplanting with an alternative tree crop. The first of these methods is unlikely to be of practical application. The average cacao farm is poorly maintained and, to be effective, pruning would need to be enforced by legislation. In some instances, trees would have to be so severely cut that selective thinning would be more appropriate. The other two methods could be incorporated with the planting of new material. Recommendations involving changes in cultural practice are not untimely, in view of the current replanting of farms which have been clear-felled for virus control; selected, high-yielding varieties are available to farmers who are prepared to return their land to cacao cultivation, and guidance is given by the Department of Agriculture. So far, agronomic studies to investigate the effect of spacing on yield (Benstead, 1957) have provided inconclusive results. The advantages of wider spacing must be further considered in relation to the importance of a closed canopy in preventing attack by cacao Mirids, and the probable increase in aerial movement of the mealybugs resulting from increased ventilation at canopy level; this aspect of vector movement is considered in a further communication. These problems might be overcome by interplanting with a secondary tree crop. Coffee would appear to be the most suitable crop for this purpose. It requires light shade and in East Africa is a food-plant for mealybugs (*Planococcus kenyae* (Le Pelley) and *Ferrisiana virgata* (Ckll.) (Haarer, 1956, both cited as *Pseudococcus*). In Ghana, coffee is planted by farmers, though on an uneconomic scale, and grows favourably under conditions encountered in the cacao-growing areas. Interplanting with this crop would not only retain the desirable closed, interlocking canopy, but vectors moving from diseased cacao might lose their infectivity by feeding on a plant which is not susceptible to cacao viruses; this suggestion is substantiated by the work of Posnette & Strickland (1948) and by Posnette & Robertson (1950), which showed that feeding mealybugs lose their infectivity in less than about an hour.

The potential losses from the spread of swollen-shoot disease in Ghana, through the inability of farmers to co-operate in the removal of latently infected contact trees, are so great that the introduction of mixed cultivation would appear highly desirable. The development of an additional economic crop would provide a safeguard to the economy of a country which depends almost entirely for its revenue on the annual crop of raw cocoa.

Summary.

An examination was made of the movements of *Pseudococcus njalensis* Laing, the dominant vector of swollen-shoot disease, on cacao in Ghana. The mobile population is composed almost entirely of first-instar nymphs (92%). Movement is initiated at about 23·5°C. and activity becomes more pronounced at higher temperatures. Movement is maximal during mid-afternoon when many hundreds of insects become mobile on heavily infested trees. The density of mobile mealybugs increases from the base of the trunk and reaches a maximum at a few feet below the top of the canopy. Under experimental conditions, nymphs walked at least 28 ft. in search of favourable feeding sites and their dispersion increased proportionately with the number of canopy bridges. On cacao, adults are occasionally carried by the ant, *Crematogaster striatula* Emery.

Using insects labelled with radioactive phosphorus, the assumption was confirmed that *P. njalensis* is capable of walking from tree to tree *via* the canopies of farmers' cacao. In a plantation of 8-year-old Amelonado cacao, 40 per cent. of the branches were in contact at 4-ft. spacing and about 20 per cent. at spacings between 5 and 7½ ft. No branches were in contact where the trees were spaced more than 12 ft. apart. At the closest spacing, the ratio between the number of mobile mealybugs that reached adjacent contact trees and those that did not was about 9:100, this ratio being reduced to 1 or 2:100 amongst trees growing 5 to 7½ ft. apart.

The significance of the movement of mealybugs in the canopy in relation to virus spread is emphasised. Methods of preventing vector dispersal by pruning, wide spacing and interplanting with a secondary tree crop are discussed. The importance of a closed canopy in preventing attack on the trees by MIRIDAE is stressed.

Acknowledgements.

The writer wishes to thank Messrs. E. S. Korangteng, C. Owusu and E. Y. Donkor for their assistance in the field. Acknowledgement is made to Dr. A. H. Ward, Physics Department, University College, Ghana, for advice in connection with the experiment using radioactive insects.

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AN ILLUSTRATED KEY FOR IDENTIFICATION OF LARVAE OF THE COTTON-PEST SPECIES OF *PECTINOPHORA* BUSCK AND *PLATYEDRA* MEYRICK (LEPIDOPTERA, GELECHIIDAE).

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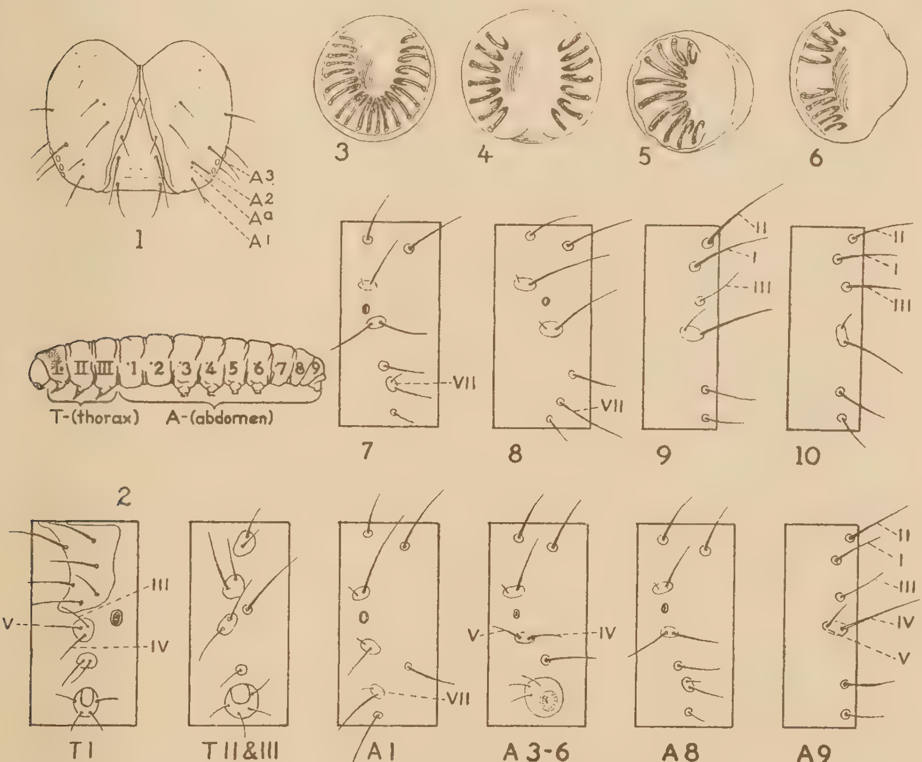
The cotton stem moth, *Platyedra vilella* (Zeller), was not known to occur in the United States prior to 1951. In August of that year, larvae of the species were found infesting hollyhock plants at Mineola, New York, by J. H. Maheny, a plant quarantine inspector of the port of New York. Adults were reared from



Figs. 1–10.—Larval characters of *Platyedra* spp. and *Pectinophoro* spp. *Platyedra vilella*: (1) dorsal aspect of head capsule; (2) body setal chart; (7) eighth abdominal segment; (9) ninth abdominal segment. *P. malvella*: (8) eighth abdominal segment. *Pectinophora gossypiella*: (3) crochets on abdominal proleg; (5) crochets on anal leg; (10) ninth abdominal segment. *P. scutigera*: (4) crochets on abdominal proleg; (6) crochets on anal leg.

additional material collected the following year, an indication that the species had become established. How or when *P. vilella* was introduced has not been determined, but doubtless it was only recently.

Pectinophora gossypiella (Saunders), *Pectinophora scutigera* (Holdaway) and *Platyedra vilella* are major pests of cotton in various parts of the world, and the possibility of their being introduced into new areas has become much more likely with faster means of transportation and the increase in travel and commerce between widely separated regions. Although not a common pest of cotton, a closely related species, *Pectinophora malvella* (Hübner), has been recorded from cotton and is also treated, since its larvae are easily confused with those of the pest species. The following key will serve to distinguish the larvae of these four species from each other and also separate them from all others, known to me, that feed on cotton in the field. The setal charts are diagrammatic, with symbols applied only to those structures referred to in the key. The characters used in the key are applicable to all instars, except the first.

Key.

1. Head with anterior puncture (Aa) between anterior setae A_1 and A_2 but closer to A_2 than to A_1 (fig. 1). Pre-spiracular group of prothorax with 3 setae (fig. 2, T I). First abdominal segment with only 2 setae in group vii (fig. 2, A_1). Abdominal proleg-bearing segments with seta iv approximate to seta v, much below level of spiracle (fig. 2, A_{3-6}); crochets uniordinal, arranged in a penellipse (fig. 3) or two transverse bands (fig. 4). Ninth abdominal segment with seta i approximately equidistant from setae ii and iii, and in line or nearly so (fig. 2, A_9); only 2 setae (iv and v) of lateral group present, seta vi absent (fig. 2, A_9). Anal segment without an anal fork. * *Pectinophora* and *Platyedra* ... 2
   Not as above .... Other species
2. Seta iii of ninth abdominal segment modified, weaker and slenderer than seta i or ii (fig. 9) 4
   Seta iii of ninth abdominal segment not modified, as strong as seta i or ii (fig. 10) 3
3. Crochets on abdominal proleg-bearing segments (A_{3-6}) uniordinal and arranged in a penellipse (fig. 3); on anal leg not interrupted medially, continuous (fig. 5) .... *Pectinophora gossypiella* (Saund.)
   Crochets on abdominal proleg-bearing segments (A_{3-6}) arranged in two transverse bands (fig. 4); on anal legs interrupted medially (fig. 6) .... *Pectinophora scutigera* (Hold.)
4. Eighth abdominal segment with 2 setae in group vii (fig. 7) .... *Platyedra vilella* (Zell.)
   Eighth abdominal segment with vii of only 1 seta (fig. 8) .... *Pectinophora malvella* (Hb.)

Acknowledgement.

The drawings for illustrations were made by Arthur D. Cushman, Agricultural Research Service, U.S. Department of Agriculture.

* *Mometa zemiodes* Durrant may also run to this category; its larva is not available for examination.

REARING AND CULTURING *MUSCA SORBENS* WIED. IN THE LABORATORY.

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and

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Musca sorbens Wied. is of considerable medical importance as being largely concerned with the transmission of conjunctivitis or trachoma (West, 1953). In Egypt, the relation of this fly to eye diseases has recently been investigated by the present authors (Hafez & Attia, 1958), and the results obtained have clearly demonstrated that this species is the main vector of ophthalmias in that country.

Workers in the Middle East have experienced a great difficulty in raising and maintaining cultures of *M. sorbens* in the laboratory owing to the fact that this fly breeds there almost exclusively in human excrement, thus rendering its rearing an unpleasant and offensive undertaking. This state of affairs has been recently emphasised by West (1953), in his report to the WHO on the problem of fly control in the East Mediterranean region, who further added that large-scale investigations on the biology of this species will continue to be rare until new techniques are developed, the aim being, primarily, to eliminate the use of human faeces as oviposition and early larval habitats.

Bearing this in mind, several artificial media were tested for their suitability as larval breeding media. The following method for rearing *M. sorbens* in the laboratory proved the most satisfactory of those tried out.

A petri dish (9 cm. in diameter and 2 cm. in height) containing a piece of cotton-wool moderately soaked in diluted milk (2 volumes milk added to 1 volume water) was placed, together with a water fountain and two sugar cubes, in the breeding cage with the adult flies. These laid their eggs on the milk pad when the latter was at least one day old. Only small numbers of eggs were usually laid. When numerous eggs were required for maintaining large colonies, a small quantity of human excrement (10–15 g.) was substituted for the milk pad. The eggs were transferred to a small jam jar containing a mixture of coarse wheat bran (120 g.) and diluted milk (240 g.). The milk and the bran had been thoroughly mixed and loosely packed before addition of the eggs. The jar was tightly covered with muslin and kept in the incubator at 27–28°C. Fully grown healthy larvae were obtained after about three days. On the fourth day, pupation usually started. Prior to pupation, a dry layer of sand or wheat bran was placed on the top of the culture to provide a suitable dry medium for pupating larvae. When the culture was 5–6 days old, it was tipped into a large basin containing water and stirred gently with a glass rod. The mixture was then allowed to stand for about five minutes and the floating puparia were then carefully skimmed off the water surface by means of gauze scoops and were dried on an absorbent surface (*e.g.*, blotting paper) and kept in a well aerated place. The average weight of a puparium produced in this medium was somewhat less than that of one produced in human excrement (Table I). The emerging adults were quite healthy and normal and were transferred to the breeding cage to maintain the stock.

The output of this milk-and-bran mixture was found to be distinctly high; thus, 30 g. of the mixture could yield up to 260 healthy full-grown larvae. Precaution was taken to avoid rearing too small a number of larvae in a given quantity of the mixture, otherwise mould formation (Born, 1954) and acid fermentation would both appear and render the breeding medium unfavourable for the developing larvae.

TABLE I.

Average weights of puparia, and other data, for *Musca sorbens* reared on different media.

Breeding medium	Av. weight of puparium (mg.)	Av. width of mesonotum (mm.)	Av. total duration from egg to adult (days)
Milk-and-bran mixture ..	11·80	1·94	8·4
Alfalfa mixture	6·6	1·62	8·6
Human excrement	14·2	1·98	8·2

All experiments at 27–28°C.

Among other media tested for breeding *M. sorbens* in the laboratory were alfalfa mixtures (Grady, 1928; Richardson, 1932; Basden, 1947). The eggs, after being deposited on one-day-old milk pads or on human excrement, were added to a mixture of 20 g. dry lucerne meal, 40 g. wheat bran, 1 g. yeast, 1·6 cc. Vidamalt (a proprietary product, containing vitamins A, B and D in malt extract, practically the same as Diamalt used by Richardson) and 90 cc. water. Larvae, pupae and adults were successfully bred from this mixture but its output was distinctly lower than that of the milk-and-bran mixture, the average weight of a puparium obtained by this method was little more than half that of a puparium reared on the milk-and-bran mixture (Table I), and the emerging flies were all undersized.

Plain milk was also tested as a larval rearing medium. It was found that eggs laid on one-day-old milk pads hatched successfully into larvae, but this medium, though it has proved suitable for rearing the house-fly, *M. domestica* L. (Hafez, 1948), cannot be advocated for raising and maintaining adequate cultures of *M. sorbens* in the laboratory since only a small percentage of the eggs deposited succeeds in completing development, and the emerging adults are considerably undersized.

Summary.

Several artificial media were tested in an attempt to eliminate the use of human faeces as oviposition and early larval habitats for breeding *Musca sorbens* Wied. in the laboratory. Eggs, laid on cotton-wool pads moistened with diluted milk or, preferably, on small quantities (10–15 g.) of human excrement, were transferred to the breeding medium. The best of those tested was a mixture of coarse wheat bran (120 g.) and diluted milk (240 g.), which yielded normal healthy larvae and adults. The average weight of a puparium produced in this medium was somewhat less than that of one produced in human excrement.

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INHERITANCE OF ALDRIN RESISTANCE IN THE INDIAN HOUSE-FLY, *MUSCA DOMESTICA NEBULO* F.

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A number of investigations have been made on the inheritance of insecticide resistance in *Musca domestica* L. Bruce & Decker (1950) tested the offspring of reciprocal crosses between DDT-resistant and normal flies and concluded that a polygenic factor was responsible for the hereditary transmission of such a resistance. This theory of multiple-gene inheritance for resistance has been supported by a number of workers including Busvine & Khan (1955) who made reciprocal crosses between a strain of *M. domestica* that was resistant to γ BHC and one that was non-resistant, and observed indications of a multifactorial heredity.

Harrison (1951), on the other hand, found a single-gene inheritance for DDT resistance in *M. domestica*—" She, however, used the time before knockdown as an index of resistance which is not always correlated with resistance to the lethal effect of DDT and it is just possible that it may be inherited by a different mechanism " (Busvine, 1953). Keiding in 1953 studied the knockdown of flies following tarsal contact with DDT and found strong indications that the major differences between resistant and susceptible strains of flies were due to a simple, incompletely recessive autosomic genetic character.

The contradictory results cited above depend on a number of factors. Varying heterozygosity has been observed by different workers (Bruce & Decker, 1950; Harrison, 1951; Pimentel, Schwardt & Dewey, 1954) in case of resistant strains either selected in the laboratory by exposing susceptible flies to sublethal doses or prevalent in nature due to indiscriminate insecticidal operations. Exposing a large population of flies to insecticidal residues under laboratory conditions certainly differs from selection in nature, where the selection pressure is not so high. It is also possible that resistance to DDT taken up by tarsal contact may

TABLE I.

Results of tests on batches of parental flies from resistant and non-resistant colonies.

Strain	Proportions of flies killed by different concentrations of aldrin				
	0·0005%	0·001%	0·005%	0·01%	0·05%
Resistant male ..	0/54 (0·0%)	10/60 (16·66%)	14/56 (25·0%)	24/36 (66·66%)	54/54 (100·0%)
Resistant female ..	0/70 (0·0%)	0/38 (0·0%)	8/50 (16·0%)	24/46 (52·17%)	68/68 (100·0%)
Normal male	36/56 (64·28%)	34/40 (85·0%)	44/48 (91·66%)	64/64 (100·0%)	24/24 (100·0%)
Normal female ..	24/60 (40·0%)	19/36 (52·77%)	40/56 (71·42%)	66/66 (100·0%)	20/20 (100·0%)

be inherited by a mechanism different from that transmitting the ability to survive topical applications (Harrison, 1953). Again, the results based on knockdown studies are never in agreement with those calculated on mortality counts, for a particular insect paralysed by a certain dose of a chemical may revive after some time and be able to survive till mortality counts are made.

A review of the literature shows that most of the studies on the inheritance of insecticide resistance have been made with DDT-resistant strains of *M. domestica* and very little attention has been paid to a study of the phenomenon in other forms of the species and with reference to different insecticides. The present work was, therefore, undertaken on the inheritance of aldrin resistance in the Indian house-fly, *Musca domestica nebulo* F.

Method and Materials.

A laboratory-raised aldrin-resistant strain of *M. d. nebulo* was compared with a non-resistant strain of the same species at a temperature of $28 \pm 1°C$. (Table I). Reciprocal crosses were made between the two strains and two sets of experiments were performed. In the first set, individual flies of the two strains were crossed, while in the other, mass crosses were made between resistant and normal strains.

Puparia of the resistant and normal strains were kept individually in small glass vials and the flies sexed on emergence. Newly emerged flies were given milk

TABLE II.

Results of tests on groups of female flies in the progenies of various resistant × non-resistant individual cross-matings.

Generation	Original cross		Proportions of flies killed by different concentrations of aldrin				
	Type	Pair no.	0·0005%	0·001%	0·005%	0·01%	0·05%
F_1	♂N × ♀R	1	0/12	0/10	3/13	8/14	17/17
		2	0/3	1/10	3/18	5/10	24/24
		3	0/6	0/5	8/24	8/13	12/12
	♂R × ♀N	1	0/5	1/12	0/6	7/12	1/1
		3	0/8	1/9	3/8	5/10	14/14
F_2	♂N × ♀R	1	0/24	1/9	2/6	8/12	11/11
		2	0/12	0/4	2/9	9/16	8/8
		3	1/8	2/11	3/11	4/7	10/10
	♂R × ♀N	1	0/12	2/12	4/18	9/17	5/5
		3	0/10	0/8	3/10	8/12	12/12
F_3	♂N × ♀R	1	1/6	2/8	5/8	10/10	12/12
		2	2/4	2/7	5/10	12/15	12/12
		3	3/13	2/8	5/14	6/10	11/11
	♂R × ♀N	1	Died —	—	—	—	—
		3	Died —	—	—	—	—
F_1	All data		0/34 (0·0%)	3/46 (6·52%)	17/69 (24·63%)	33/59 (55·93%)	68/68 (100·0%)
F_2	All data		1/66 (1·51%)	5/44 (11·36%)	14/54 (25·92%)	38/64 (59·37%)	46/46 (100·0%)
F_3	All data		6/23 (26·08%)	6/23 (26·08%)	15/32 (46·87%)	28/35 (80·0%)	35/35 (100·0%)

and sugar and the families built up by each couple paired were kept separately in 4-in. sleeve cages. Out of 10 families (five each of ♂N × ♀R and ♂R × ♀N) thus formed, three from the former and two from the latter type survived. Other pairs either died or did not oviposit. Most of the F_1 flies from each family were tested and only a few individuals were saved to raise F_2 flies. The same procedure was followed in F_2 and subsequent generations.

In view of the lack of a technique for measuring the resistance of an individual fly to a poison, the level of resistance of parental as well as hybrid colonies could be established only in terms of mortality, and, for this reason, groups of flies were tested in every case. Topical applications of oil solutions of aldrin were made on the dorsum of the thorax of each fly by means of a syringe. The size of the drop was kept constant but the concentration of aldrin varied with different experiments. The flies were sexed at the time of treating and those belonging to the same sex were kept in a separate cage. Fresh food was given to the treated flies and mortality counts were made 24 hours after treatment.

Results.

The groups of male and female hybrids of either cross, ♂N × ♀R and ♂R × ♀N, gave similar results, indicating that aldrin resistance in *M. d. nebulo* was exhibited by the progeny of male and female hybrids irrespective of whether it was

TABLE III.

Results of tests on groups of male flies in the progenies of various resistant × non-resistant individual cross-matings.

Generation	Original cross		Proportion of flies killed by different concentrations of aldrin				
	Type	Pair no.	0·0005%	0·001%	0·005%	0·01%	0·05%
F_1	♂N × ♀R	1	0/21	2/15	4/10	16/18	11/11
		2	0/16	2/11	6/9	14/17	5/5
		3	0/7	0/3	8/16	11/12	20/20
	♂R × ♀N	1	0/10	2/9	1/4	4/5	7/7
		3	0/15	0/6	3/5	9/13	22/22
F_2	♂N × ♀R	1	2/10	3/14	8/14	11/12	19/19
		2	1/8	1/4	4/8	11/11	15/15
		3	2/8	1/3	6/12	9/10	3/3
	♂R × ♀N	1	1/10	5/16	8/16	11/13	10/10
		3	1/11	1/5	7/12	5/6	12/12
F_3	♂N × ♀R	1	3/8	6/12	5/6	8/8	7/7
		2	2/8	2/6	5/9	20/20	15/15
		3	3/10	3/8	5/7	12/12	11/11
	♂R × ♀N	1	Died —	—	—	—	—
		3	Died —	—	—	—	—
F_1	All data		0/69 (0·0%)	6/44 (13·63%)	22/44 (50·0%)	54/65 (83·07%)	65/65 (100·0%)
F_2	All data		7/47 (14·89%)	11/39 (28·20%)	33/62 (53·22%)	47/52 (90·38%)	59/59 (100·0%)
F_3	All data		8/26 (30·75%)	11/26 (42·30%)	15/22 (68·18%)	40/40 (100·0%)	33/33 (100·0%)

the male or the female parent that was resistant to aldrin (Tables II, III, IV and V). That the phenomenon is not sex linked is supported by the results, obtained on testing individual flies of the two strains, shown in the Tables mentioned above.

TABLE IV.

Results of tests on groups of female flies in the progenies of resistant × non-resistant mass cross-matings.

Generation	Type	Proportions of flies killed by different concentrations of aldrin				
		0·0005%	0·001%	0·005%	0·01%	0·05%
F_1	♂N × ♀R	0/40	0/24	4/20	13/23	16/16
	♂R × ♀N	0/38	0/28	6/22	22/36	30/30
F_2	♂N × ♀R	4/31	4/15	6/21	18/27	25/25
	♂R × ♀N	2/20	0/28	12/32	24/34	15/15
F_3	♂N × ♀R	4/17	5/17	9/18	7/10	17/17
	♂R × ♀N	0/42	6/30	12/24	21/30	40/40
F_4	♂N × ♀R	6/22	15/39	28/52	19/26	25/25
	♂R × ♀N	5/40	12/42	15/28	12/17	19/19
F_5	♂N × ♀R	12/36	16/36	27/27	44/44	31/31
	♂R × ♀N	6/26	15/32	20/32	52/52	32/32
F_1	All data	0/78 (0·0%)	0/52 (0·0%)	10/42 (23·80%)	35/59 (59·32%)	46/46 (100·0%)
F_2	All data	6/51 (11·76%)	4/43 (9·30%)	18/53 (33·96%)	42/61 (68·86%)	40/40 (100·0%)
F_3	All data	4/59 (6·77%)	11/47 (23·40%)	21/42 (50·0%)	28/40 (70·0%)	57/57 (100·0%)
F_4	All data	11/62 (17·74%)	27/81 (33·33%)	43/80 (53·75%)	31/43 (72·09%)	44/44 (100·0%)
F_5	All data	18/62 (29·03%)	31/68 (45·58%)	47/59 (79·66%)	96/96 (100·0%)	63/63 (100·0%)

F_1 flies were slightly less resistant than the resistant parents and far more resistant than the non-resistant ones, and though the degree of resistance decreased in the F_2 generation, it was still nearer to the resistant parents. It seems, therefore, that aldrin resistance in *M. d. nebulo* is a phenomenon of multifactorial heredity, a conclusion further substantiated by the fact that hybrids in all the tests performed were somewhat more variable in their susceptibility than the parental stock.

It is concluded from the foregoing results that aldrin resistance in *M. d. nebulo* is controlled by a multiple-gene factor, and that the phenomenon is not sex linked.

Summary.

The inheritance of aldrin resistance in the Indian house-fly, *Musca domestica nebulo* F., was studied by making reciprocal crosses between individual as well as

groups of flies of an aldrin-resistant and a non-resistant strain of the subspecies at 28 ± 1°C. The offspring of all the families thus formed were tested by the topical application of constant-volume drops of various concentrations of aldrin solution in oil to the dorsum of thorax of groups of flies. Mortality counts were made 24 hours after treatment. The results obtained indicated a multifactorial heredity for aldrin resistance in *M. d. nebulo*. The phenomenon was found not to be sex linked.

TABLE V.

Results of tests on groups of male flies in the progenies of resistant × non-resistant mass cross-matings.

Generation	Type	Proportions of flies killed by different concentrations of aldrin				
		0·0005%	0·001%	0·005%	0·01%	0·05%
F_1	♂N × ♀R	3/24	6/20	10/26	26/28	25/25
	♂R × ♀N	3/28	8/28	10/24	32/36	34/34
F_2	♂N × ♀R	4/14	12/30	21/45	51/51	35/35
	♂R × ♀N	6/32	7/27	12/24	34/36	38/38
F_3	♂N × ♀R	4/11	6/11	18/24	22/22	24/24
	♂R × ♀N	6/24	12/30	18/28	33/35	19/19
F_4	♂N × ♀R	14/33	15/27	32/36	34/34	31/31
	♂R × ♀N	7/24	10/22	17/24	19/19	33/33
F_5	♂N × ♀R	12/28	24/32	25/25	28/28	59/59
	♂R × ♀N	14/26	20/28	42/42	38/38	41/41
F_1	All data	6/52 (11·53%)	14/48 (29·16%)	20/50 (40·0%)	58/64 (90·62%)	59/59 (100·0%)
F_2	All data	10/46 (21·73%)	19/57 (33·33%)	33/69 (47·82%)	85/87 (97·70%)	73/73 (100·0%)
F_3	All data	10/35 (28·57%)	18/41 (43·90%)	36/52 (69·23%)	55/57 (96·49%)	43/43 (100·0%)
F_4	All data	21/57 (36·84%)	25/41 (51·02%)	49/60 (81·66%)	53/53 (100·0%)	64/64 (100·0%)
F_5	All data	26/54 (48·14%)	44/60 (73·33%)	67/67 (100·0%)	66/66 (100·0%)	100/100 (100·0%)

Acknowledgements.

The author wishes to express his grateful thanks to Professor M. B. Mirza, Head of the Department of Zoology, for his valuable criticism and advice during the progress of this work, and to Dr. Nawab H. Khan under whose kind direction this work was undertaken.

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OBSERVATIONS ON THE BEHAVIOUR OF SOME MOSQUITOS OF THE KENYA COAST.

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From October 1949 to March 1952, mosquitos were studied at Ganda and Mambrui, two villages on the Kenya coast. Ganda was used as a control when Mambrui was sprayed with DDT in 1949. The results are recorded with special reference to biting habits as shown by 24-hour catches.

Eighty species, subspecies and varieties have been recorded at Ganda and Mambrui but only a few of these are discussed in detail in this paper. A complete list, with notes on nomenclature and variations, is given elsewhere (van Someren, Teesdale & Furlong, 1955) but it should be noted that the exact status of the *Aëdes* (*Ochlerotatus*) species, referred to here under the familiar name of *fryeri*, has not yet been decided. It should also be noted that during the present survey the significance of colour variations in *Aë.* (*Stegomyia*) *aegypti* was not appreciated and all forms were recorded under one heading. Recently, Mattingly (1957) has proposed separating *Aë. aegypti* into a type form, ssp. *formosus* (Wlk.) and var. *queenslandensis* (Theo.); the last two forms are known to occur on the Kenya coast.

The catches made are considered separately and classified as follows:—(i) net catches in the bush, (ii) space-spraying catches in houses, (iii) window-trap catches and (iv) 24-hour catches.

Ganda (fig. 1) is a small inland village about five miles from Malindi on the Kenya coast; it consists of mud-and-wattle huts with palm-thatched roofs. The huts are scattered among coconut plantations and there are a few mud-brick houses with galvanised-iron roofs along the road which passes through the village. The local natives are Giriama who are mainly cultivators; in the village there are also Arab and Swahili traders who buy and sell the produce of the plantations which includes rice, maize, cotton, fruit and nuts.

Mango, *Citrus*, cashew-nut (*Anacardium*) and kapok (*Ceiba*) trees have been planted among the coconut palms and there are a few patches of pineapple and bananas. Clumps of weedy bush occur on waste ground around dilapidated huts and along paths. Around the huts there are a few tall indigenous trees with occasional patches of bamboo, *Dracaena* and screw pines (*Pandanus*). On the fringes of the coconut plantations there are groves of mango and cashew-nut trees, interspersed with tall trees and the odd doum palm (*Hyphaene*). The ground here has a fairly dense covering of long grass and around most of the trees there is low scrubby bush. Beyond the groves are open grasslands with scattered clumps of trees. In the grass, there grow short herbs, creeping plants, young doum palms, clumps of woody bush and tall isolated trees. Small areas of grassland are cleared and used mainly for the cultivation of cotton. To the north-west of the village there is a large depression which has some permanent water and is flooded in the wet season.

Mambrui (fig. 2) is an old Arab village on the sea coast, about 10 miles north of Malindi; it is windswept, with little shade. On the sea front to the north and south there are sand dunes covered with scrub. Behind the dunes, for about ¼ mile inland, the bush is low and dense in the south, and sparse in the north,

where there is also a large swampy area. West of the village there is scattered bush and grazing land with a belt of large trees, mainly mango. Beyond this the land is cultivated and rises steeply to about 240 ft. The inhabitants are Arab and Swahili cultivators and traders.

The climate of the Kenya coast is influenced by the monsoons. The main rainfall is from April to June, with lighter rain between October and December;

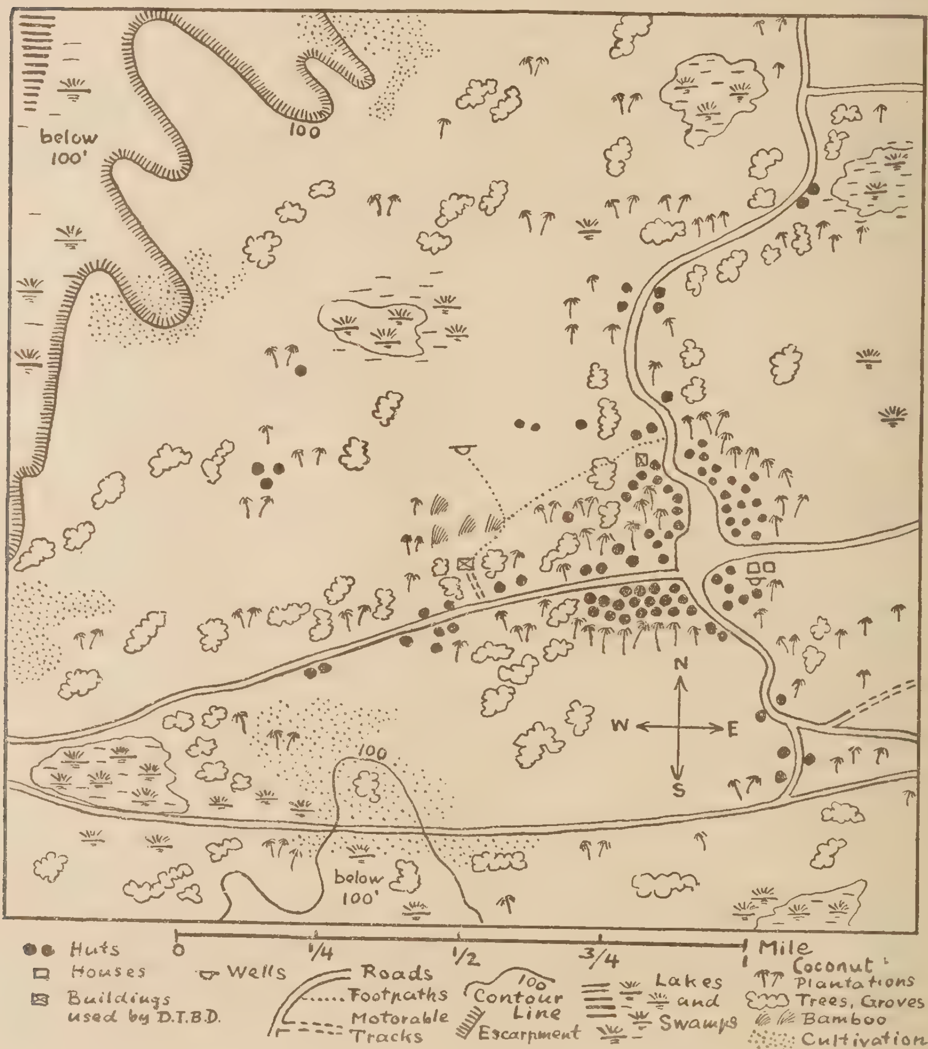

Fig. 1.—Map of Ganda.

the only dry months are January and February. The average rainfall over 58 years for Malindi is 40·88 in. and 1949 was a dry year with only 21·1 in. In 1950, there were 36·27 in. and 1951 was a year of heavy rain with 71·34 in., of

which 27·21 in. fell in May. The temperature does not vary much at Malindi, the mean maximum being about 86°F. with a minimum of 73°F. March is usually the hottest month and the lowest temperatures are recorded in July. The average relative humidity is fairly high throughout the year, ranging from 70 to 89 per cent.

Fig. 2.—Map of Mambrui.

At Ganda and Mambrui, from February 1950 to May 1951, wet and dry bulb readings were taken hourly during the 24-hour catches in "bush", "house" and "compound" (see below, p. 652). The range of temperature and humidity is shown in Table I and the average figures for each hour to the nearest whole number are plotted in fig. 3.

TABLE I.

Range of temperature and humidity readings at Ganda and Mambrui.

	Mambrui				Ganda							
	House		Bush		Ordinary house		Rented house		Compound		Bush	
	°F.	%R.H.	°F.	%R.H.	°F.	%R.H.	°F.	%R.H.	°F.	%R.H.	°F.	%R.H.
1950 : Feb.	79–86	73–83	77–87	66–87	—	—	79–88	68–81	75–89	57–86	76–90	57–87
,, Mar.	82–93	65–84	80–94	57–87	81–90	64–83	82–88	70–84	79–93	53–91	71–91	52–95
,, Apr.	81–84	80–84	75–89	70–100	74–85	73–91	80–87	66–84	—	—	75–87	70–100
,, May	79–82	79–91	73–85	72–100	79–84	73–87	79–84	75–84	76–84	82–94	77–84	73–91
,, June	76–81	75–87	72–80	87–100	72–81	64–95	75–81	68–87	73–83	65–91	71–76	74–100
,, July	77–80	75–83	71–78	82–100	73–79	75–86	72–77	82–91	72–80	78–91	69–75	91–100
,, Aug.	78–80	75–83	73–84	69–91	73–78	75–91	73–81	68–91	69–82	65–87	72–80	75–95
,, Sept.	—	—	—	—	71–83	65–91	74–81	68–91	75–81	75–96	68–82	65–95
,, Oct.	80–82	75–83	74–89	56–91	77–87	60–91	76–88	57–83	76–89	54–87	69–84	66–95
,, Nov.	80·5–85	73–84	72–85	61–95	73–87	61–96	78–84	72–96	74–88	57–91	70–85·5	66–100
,, Dec.	82–86	73–84	74–89	73–88	74–90	61–87	78–89	51–88	78–91	55–87	73–85	62–95
1951 : Jan.	80–84	73–84	71–88	57–91	—	—	—	—	—	—	—	—
,, Feb.	82–86	59–84	78–90	57–91	74–90	54–91	76–86	60–87	79–90	57–83	71–87	51–95
,, Mar.	—	—	—	—	78–90	57–87	79–88	60–83	80–92	53–83	73–87	63–96
,, Apr.	80–89	64–87	73–87	63–100	77–87	66–96	80–86	73–87	79–89	64–87	75·5–82·5	77·5–98
,, May	78·5–82	80–87	77–87	61–91	72–83	78–95	75–78	87–96	77–82	61–91	72·5–84	71·5–100

The temperature and humidity are fairly constant throughout the night and until about an hour after sunrise. From 07 hr. there is a gradual rise in temperature and a sharp drop in humidity until the hottest and driest period is reached about midday; there is little change in the afternoon until about an hour before

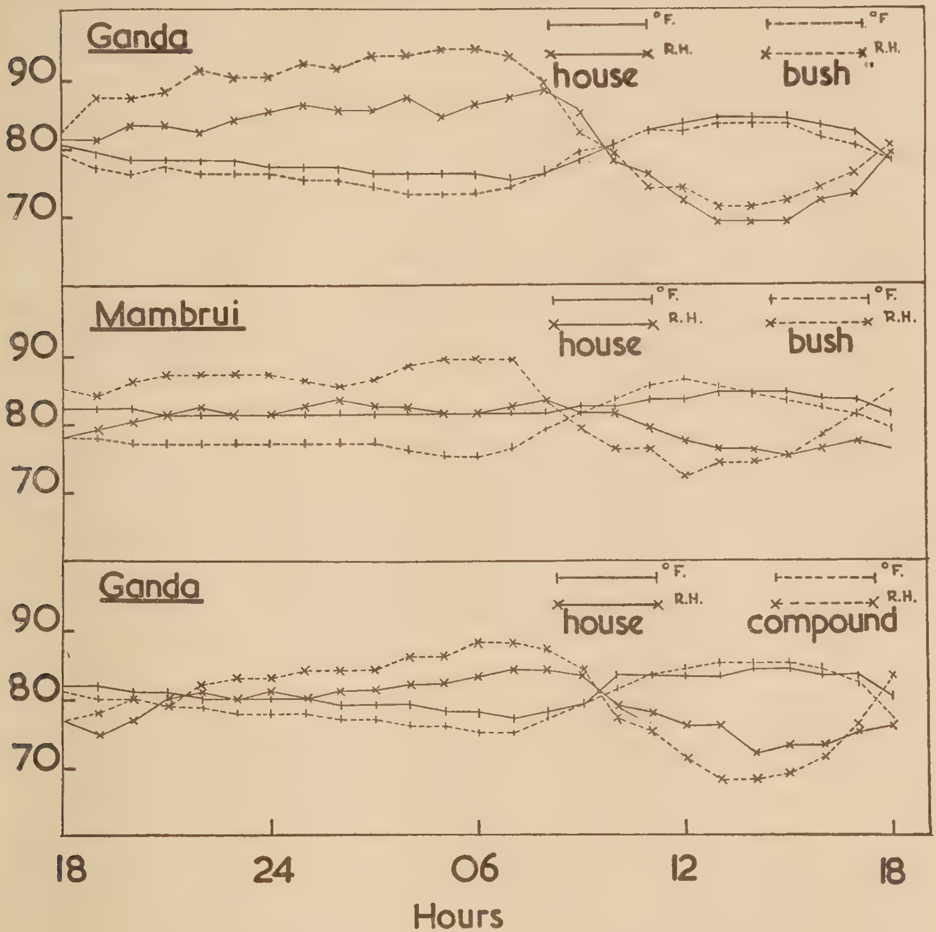

Fig. 3.—Humidity and temperature curves for Ganda and Mambrui.

sunset. At Ganda there is more variation in temperature and humidity than at Mambrui and in both villages the bush readings are more variable than those in the houses. The bush temperatures at Ganda are on an average 1–3° lower than those at Mambrui and the humidity is slightly higher. During the day, the temperature and humidity is much the same in the houses and in the bush in both villages but at night the temperature is higher and humidity is lower in the houses than in the bush.

The Net Catches in the Bush.

These were done from May 1951 to March 1952 by four Africans who swept the bush with nets daily, starting at 07 hr. and finishing at noon; all types of

TABLE II.

Common species: net catches in the bush, Ganda and Mambrui, May 1951–March 1952.

	Anopheles (Anopheles) coustani tenebrosus Dön.	*Anopheles (Myzomyia) funestus* Giles	*Anopheles (Myzomyia) gambiae* Giles	*Taeniorhynchus (Mansonioides) africanus* (Theo.)	*Taeniorhynchus (Mansonioides) uniformis* (Theo.)	*Aëdes (Ochlerotatus) fryeri**	*Aëdes (Stegomyia) aegypti**	*Aëdes (Stegomyia) subargenteus* Edw.	*Aëdes (Stegomyia) woodi* Edw.	*Aëdes (Stegomyia) simpsoni* (Theo.)	*Aëdes (Stegomyia) metallicus* (Edw.)	*Aëdes (Aëdimorphus) argenteopunctatus* (Theo.)	*Aëdes (Aëdimorphus) tarsalis* (Newst.)	*Aëdes (Aëdimorphus) albocephalus* (Theo.)	*Aëdes (Aëdimorphus) cumminsi mediopunctatus* (Theo.)	*Aëdes (Banksinella) albothorax* (Theo.)	*Aëdes (Banksinella) albicosta* (Edw.)	*Aëdes (Banksinella) ellinorae* Edw.	*Aëdes (Dunnius) michaelikati* van Som.	*Aëdes (Skusea) pembaensis* (Theo.)	*Culex (Lutzia) tigripes* Grp.	*Culex (Culex) poicilipes* (Theo.)	*Culex (Culex) annulioris* Theo.	*Culex (Culex) sitiens* Wied.	*Culex (Culex) univittatus* Theo.	*Culex (Culex) simpsoni* Theo.	*Culex (Culex) pipiens fatigans* Wied.	*Culex (Culex) invidiosus* Theo.	*Culex (Culex) perfuscus* Edw.	*Culex (Culex) guiarti* Blanch.	*Culex (Culex) weschei gediensis* Edw.	*Culex (Culex) grahami* Theo.
May	–	–	–	3	1	27	2	–	–	3	38	–	–	2	1	–	9	–	5	–	7	–	–	–	5	–	1	21	43	–	–	–
June	2	1	10	2	3	–	4	–	286	7	–	1	1	1	–	8	6	–	–	5	11	2	2	3	1	–	–	145	43	1	25	1
July	15	–	–	2	3	–	7	–	102	28	15	11	1	21	2	5	7	–	1	9	5	1	14	5	–	–	–	372	34	32	119	29
Aug.	5	–	1	22	35	–	11	5	191	25	1	5	1	46	6	1	4	–	1	6	13	3	23	2	23	19	–	243	6	29	75	40
Sept.	3	2	–	22	33	–	1	7	193	–	–	3	–	7	4	–	6	–	2	3	10	15	24	1	14	26	1	121	4	334	34	27
Oct.	–	–	–	34	29	–	2	5	181	–	–	50	2	132	8	4	33	–	2	3	3	16	17	4	21	3	1	91	2	347	6	14
Nov.	15	267	102	142	84	16	13	6	179	17	12	8	8	208	8	166	147	48	10	40	–	8	2	1	6	–	3	128	66	165	4	13
Dec.	12	112	2	227	108	–	4	7	324	–	2	30	5	125	1	60	69	–	8	9	9	19	5	8	2	1	4	7	59	83	–	2
Jan.	1	33	–	487	158	–	1	1	43	–	1	–	–	94	–	19	20	1	–	–	3	4	1	9	1	1	1	6	4	10	–	–
Feb.	–	–	–	552	555	–	–	–	17	3	–	–	–	5	1	6	3	–	–	–	1	2	1	–	–	–	1	–	1	–	–	–
Mar.	–	1	–	336	219	–	–	–	27	[illegible]	[illegible]	[illegible]	[illegible]	2	[illegible]	2	1	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

bush were sampled. Sixty five species were taken in these catches. As the incidence at Ganda and Mambrui was much the same the figures for the two places have been combined. The 32 common species are listed in Table II, and a further 33 species were taken occasionally; 18 of these were very rare.

The most productive months were the hot, humid months of November and December. Nineteen species were taken regularly but there was a seasonal fluctuation in numbers; most of them were scarce in the dry months and some in the cool season. *Taeniorhynchus uniformis* (Theo.), *T. africanus* (Theo.), *Aë. woodi* Edw., *Culex invidiosus* Theo. and *C. guiarti* Blanch. were common and *Aë. albocephalus* (Theo.), *Aë. albothorax* (Theo.) and *Aë. albicosta* (Edw.), *C. perfuscus* Edw. and *C. weschei gediensis* Edw. were fairly numerous. *Aë. aegypti* was rare and *Anopheles gambiae* Giles and *Aë. simpsoni* (Theo.) were scarce and seasonal. *Anopheles funestus* Giles appeared in large numbers in the last two months of 1951 and a few were taken in January 1952; only occasional specimens were seen during the other months despite the heavy rains early in 1951.

The Space-spraying Catches in Houses.

Once a month, from October 1949 to December 1951, 15 selected houses at Ganda and 30 at Mambrui were sprayed with pyrethrum. All mosquitos knocked down were collected and identified; the results are given in Table III. The spraying was done during the day, and while one man sprayed inside, another sprayed the eaves from outside. The floors were covered with white sheets and all doors and windows closed. Only the figures for Ganda are shown here, as few mosquitos were taken in the houses at Mambrui after they had been sprayed with DDT in October 1949.

Ten species were found resting in the houses during the day (Table III) but only four were taken in any numbers; these were *Culex pipiens fatigans* Wied., *Aë. aegypti*, *A. funestus* and *A. gambiae*. *C. p. fatigans* was very common and found at all times; its numbers dropped considerably in the hot, dry months of January and February, in the cooler months of June and July and during the heavy rain from March to May 1951. *Aë. aegypti* was constantly present in small numbers. *A. gambiae* was taken in fairly large numbers after the heavy rain in 1951 though it was scarce in 1950. *A. funestus* was completely absent from the houses until the latter half of 1951 when large numbers appeared in the last four months of the year; this influx came after the exceptionally wet season early in 1951 when extensive flooding occurred.

The Window-trap Catches.

Cage traps were attached to the windows of a house in Ganda that had been rented for the work and is therefore referred to as the "rented house" and was of mud and wattle with a palm-thatched roof. There were two rooms, each with a ceiling and a window, and the main room had two outside doors. The outside doors of the hut were kept shut and a man slept in it at night. During the day the house was unoccupied, except when 24-hour catches were in progress.

It should be pointed out that, in the rented house, the population of *Aë. aegypti* was artificially increased by introducing a large drum and some earthenware pots which were continually supplied with larvae from outside.

The traps, made to fit the window frames, were about 2 ft. square and made of wire gauze on a light wooden frame. They contained a smooth gauze funnel which narrowed to a small opening inside the cage. Mosquitos were collected through a sleeve on one side of the trap. A trap attached to the inside of a window collected in-going mosquitos and one outside, out-going mosquitos. An out-going trap was attached to the west wall and an in-going trap to the south wall. Catches in each were recorded at the same time.

Attempts were made to record the different stages of the gonotrophic cycle in relation to periods of maximum and minimum activity, but the results are not included as they were not sufficiently reliable.

The out-going trap.

Thirty species were recorded in the trap but only *A. funestus*, *A. gambiae*, *T. uniformis*, *T. africanus*, *Aë. aegypti*, *C. p. fatigans* and *C. horridus* Edw. were taken regularly. A few specimens of *A. coustani tenebrosus* Dön., *C. sitiens*

TABLE III.

Space spraying in houses, Ganda.

Month	*A. funestus* ♂	♀	*A. gambiae* ♂	♀	*T. uniformis* ♂	♀	*T. africanus* ♂	♀	*Aë. aegypti* ♂	♀	*C. sitiens* ♂	♀	*C. p. fatigans* ♂	♀
1949 : Oct.	—	—	—	2	—	—	—	—	7	20	—	—	261	390
Dec.	—	—	—	1	—	—	—	—	3	11	—	—	78	125
1950 : Jan.	—	—	—	—	—	—	—	—	1	29	—	—	25	33
Feb.	—	—	—	2	—	—	—	—	1	24	—	—	18	39
Mar.	—	—	—	—	—	—	—	—	2	8	—	—	53	133
Apr.	—	—	3	10	—	—	—	—	—	6	—	12	143	218
May	—	—	—	14	—	—	—	—	1	24	—	26	102	210
June	—	—	—	1	—	—	—	—	3	9	—	6	4	21
July	—	—	—	—	—	—	—	—	12	26	—	8	13	21
Aug.	—	—	—	29	—	—	—	—	2	—	—	6	80	107
Sept.	—	—	—	2	—	—	—	—	1	2	—	4	97	177
Oct.	—	—	—	—	—	—	—	—	2	2	1	—	61	66
Nov.	—	—	1	—	—	1	—	—	3	16	—	—	96	87
Dec.	—	—	2	—	—	1	—	—	3	26	—	—	45	126
1951 : Feb.	—	—	—	—	—	—	—	—	13	28	—	—	4	4
Mar.	—	—	—	—	—	—	—	—	9	21	—	—	9	4
Apr.	—	—	—	2	—	—	—	—	16	11	—	—	2	5
May	—	—	2	17	—	—	—	—	2	27	—	—	1	2
July	—	—	7	31	—	—	—	—	1	4	—	—	1	2
Aug.	1	35	28	61	—	4	—	—	1	12	—	—	65	134
Sept.	20	281	14	26	—	7	—	3	1	14	—	—	32	57
Oct.	3	39	—	5	—	1	—	—	—	7	—	—	40	44
Nov.	6	752	24	465	—	—	—	2	—	2	—	—	40	52
Dec.	27	561	10	85	—	2	—	1	—	1	—	—	65	81
Totals	57	1668	91	753	—	16	—	6	84	330	1	62	1335	2138

In addition, 1 ♀ of *C. univittatus*, 1 ♀ of *Aë. fryeri* and 2 ♀♀ of *C. perfuscus* were taken in April 1950 and 1 ♀ of *C. perfuscus* in July 1951.

Wied., *C. decens* Theo., *C. invidiosus* and *C. perfuscus* were taken occasionally and the remaining species were only found once or twice.

Two series of catches are described in turn. The first started in July 1950 and ended on 15th August 1951; the cage was examined every four hours starting at 02 hr. local time (East African Standard Time = G.M.T. + 3). In this

series, only a few examples of *A. funestus*, *T. africanus*, *T. uniformis* and *C. horridus* were recorded; the first three species were taken between 18 and 06 hr. but *C. horridus* was found only during the day. Ninety five males and 675 females of *A. gambiae* were taken as well as 424 males and 460 females of *Aë. aegypti*, and 1,071 males and 1,708 females of *C. p. fatigans*. These three species were very active in the four hours before dawn. Between 22 and 10 hr., 69 males and 465 females of *A. gambiae* were taken and half were collected between 02 and 06 hr. *C. p. fatigans* was most active from sunset to dawn, 934 males and 1,402 females being taken between 18 and 06 hr.; 42·5 per cent. of these left between 02 hr. and dawn. *Aë. aegypti* had two waves of activity, between 14 and 18 hr. (140 males and 142 females) and 02 and 06 hr. (77 males and 103 females).

TABLE IV.

Ganda: out-going window trap, 16th August 1951 to March 1952.

	A. funestus		*A. gambiae*		*T. africanus*		*T. uniformis*		*Aë. aegypti*		*C. p. fatigans*		*C. horridus*	
Hours	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
22–02	221	1488	39	234	–	47	–	147	3	9	228	506	2	5
02–03	147	1100	23	141	–	37	–	81	1	5	159	276	–	2
03–04	139	975	25	153	–	31	1	95	1	6	135	285	1	–
04–05	75	900	14	127	–	24	–	74	1	2	116	240	2	1
05–06	65	1105	17	219	–	35	–	77	2	5	143	339	–	1
06–10	22	485	9	76	–	14	–	18	1	8	64	161	1	6
10–14	4	240	3	32	–	3	–	5	10	12	43	55	2	2
14–15	–	150	3	19	–	2	–	6	1	3	15	28	2	4
15–16	6	96	1	9	–	–	–	4	2	4	11	25	4	1
16–17	1	81	3	10	–	1	–	4	3	10	12	30	–	3
17–18	3	85	2	9	–	3	–	5	13	12	11	39	3	1
18–22	265	1021	38	95	–	39	1	100	7	17	269	378	3	4
Totals	948	7699	177	1124	–	236	2	616	45	93	1206	2362	20	30

In addition, a few specimens of the following species were taken in this trap: *A. coustani* and vars. *tenebrosus* and *ziemanni* Grünb., *A. keniensis* Evans, *Aë. fulgens* (Edw.), *woodi*, *simpsoni*, *metallicus*, *cumminsi mediopunctatus* and *C. tigripes*, *insignis* (Cart.), *nebulosus* Theo., *furlongi* van Som., *sitiens*, *duttoni* Theo., *simpsoni*, *antennatus*, *decens*, *invidiosus*, *perfuscus*, *guiarti*, *weschei gediensis* and *grahami*.

In the second series of catches between 16th August 1951 and March 1952 the results were more detailed. The same 4-hourly periods were maintained except between 02 and 06 hr. and between 14 and 18 hr., when the cages were examined hourly. The figures show (Table IV) that as in the previous series the movement of *A. funestus*, *A. gambiae*, *T. uniformis*, *T. africanus* and *C. p. fatigans* increased after 18 hr. but did not reach a peak until after 02 hr.

Between 02 and 06 hr. the numbers leaving the house were about the same every hour but there was a slight increase just before dawn. Few specimens of *Aë. aegypti* were taken in this series but as its activity increased around 18 hr. in both catches, the main peak probably occurs between 18 and 19 hr., as was shown by Teesdale (1955) for *Aë. aegypti* in Mombasa.

The in-going trap.

Two series of catches were made, in the in-going trap, at the same time as the out-going trap catches, the cage being examined daily at the same 4-hourly intervals. Very few mosquitos were attracted to the in-going trap, which collected only 289 specimens. The following six species were taken:—*A. funestus* 20 ♂♂, 97 ♀♀, *A. gambiae* 12 ♂♂, 30 ♀♀, *Aë. aegypti* 25 ♂♂, 26 ♀♀, *C. p. fatigans* 45 ♂♂, 34 ♀♀, *T. uniformis* 6 ♀♀ and *T. africanus* 1 ♀. There was no activity between 18 and 02 hr. Movement into the trap began some time between 02 and 06 hr. and, after that, activity continued throughout the day, ceasing abruptly at sunset. It seems probable that no mosquitos were caught in the trap at night because they entered the hut through cracks and crevices in the walls. Those caught during the day may have used the trap as a resting place.

The 24-hour Catches.

Four teams, supervised by a European, and consisting of two boys and one senior African, worked these catches, acting as both bait and catchers; each team did three hours on and nine hours off duty. The mosquitos coming to the bait were recorded hourly (local time). Sunset and dawn were at approximately 18 and 06 hr., respectively. Whenever possible, a catch was made monthly in each situation (see below) from October 1949 till July 1951.

At Ganda, catches were made in the rented house, which has been described above, and in an "ordinary house" which was constructed like the rented house but contained three rooms, without ceiling, and was occupied by an elderly African couple. Catches were also made in the "compound" of the rented house, and in the "bush". The "compound" was an area at the back of the house, fenced with palm leaves, which contained outhouses and a certain number of domestic animals, and a part under the eaves of the rented house where the catches were made. The "bush" catches were done on the fringe of the coconut plantations, under a mango tree, which was surrounded by low bush.

A series of 24-hour catches was also made at Mambrui in a house and in the bush. The bush catches were carried out in the low dense bush behind the sand dunes to the south of the village. Very few mosquitos were taken in the house at Mambrui after the DDT spraying campaign, thus the biting cycles for the houses are based on catches at Ganda alone.

Thirty five species were taken in these catches (Table V & figs. 4 & 5) but only 13 were taken often enough and in sufficient numbers to work out a biting cycle. Ten of these are considered, for *C. sitiens* is the subject of a separate paper, and it is not certain whether two others, *Aë. albocephalus* and *C. tritaeniorhynchus* Giles, were correctly identified in the early catches. The three species, *A. gambiae*, *Aë. aegypti* and *C. p. fatigans*, were taken often enough for a comparison to be made of bush, house and compound biting cycles and these are shown in fig. 4. The bush cycles are based on the combined Ganda and Mambrui figures. The house curve is based on the combined figures for rented and ordinary houses since the two sets of observations show no appreciable difference.

The other seven species were taken in sufficient numbers in the bush only. The biting cycles of these are shown in fig. 5, a–g, and their occurrence in the other situations is recorded in the text.

The combined results for the various hour-groups were expressed as geometric means using the method recommended by Haddow (1954), after which the figures were reduced to a percentage to facilitate comparison.*

Species biting in bush, house and compound.

Anopheles gambiae (fig. 4, a).—This species was nocturnal and was taken biting more often outside than inside. The biting cycle is very similar to that recorded by Mattingly (1949*a*) for *A. gambiae* in Uganda and Nigeria, and by Lumsden (1955) in Kenya at Taveta. The Ganda house curve in particular is very like those already mentioned and has an initial small peak just after sunset, followed by a gradual build-up with the main peak occurring in the second half of the night. The initial rise, referred to above, came between 18 and 19 hr. in the house and compound and an hour later in the bush. The main peak occurred at different times in the three situations. The house peak was between 04 and 05 hr. and the bush peak was an hour earlier; the compound differed by having a very marked peak in the hour after midnight when activity dropped in the other two situations. *A. gambiae* was most active in the bush from April to June and was more often taken biting in the houses during July and August (Table VI).

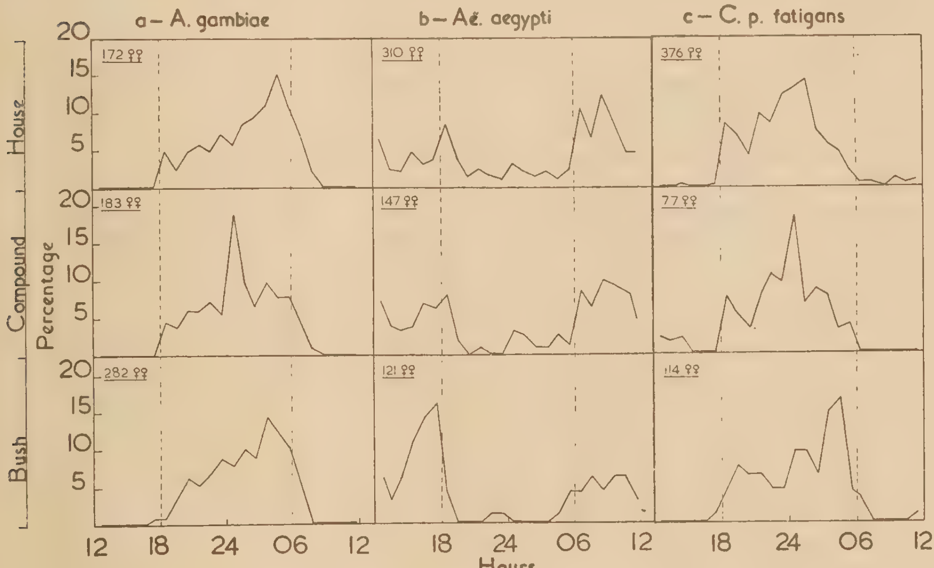

Fig. 4.—Biting cycles in bush, house and compound as shown by geometric means, reduced to percentages. Number of catches in house, 36; compound, 16; bush, 43.

Aëdes aegypti (fig. 4, b).—This was a diurnal species though small numbers bit throughout the night. Many more were taken in the house catches than in the bush but most of these were from the rented house. In Table VI, house catches include those caught biting in the rented house where breeding was artificially increased. The number caught biting in the ordinary house was very small, only 38 being taken during the monthly catches as compared with 272 from the rented house. Although only a few were taken in the ordinary house

* Detailed data for figs. 3, 4 and 5 are deposited in the Archives of the British Museum (Natural History), London, and will be available there for reference.

at Ganda, the largest number (9) was taken in July at a time when biting in the bush was low, and of the 98 examples of *Aë. aegypti* taken biting in the bush, 36 were taken in April. These seasonal habits are rather similar to those of *A. gambiae*. The biting cycles in all situations are similar and show a morning and evening peak. The house and compound curves are very alike with an initial peak an hour after dawn and a period of high activity between 08 and 10 hr. The curve was then irregular until sunset; there was a second small peak an hour after sunset and biting continued at a low level throughout the night. In the bush, the same biting rhythm occurred but the evening peak was higher than the morning one and came before sunset; biting dropped rapidly after dark and remained low throughout the night until an hour before dawn. Teesdale (1955) also noted the presence of a high evening peak in his outside catches of *Aë. aegypti* near Mombasa, and the same was observed in catches of *Aë. aegypti* in a forest near Nairobi.

It should be noted that in these catches the colour forms of *Aë. aegypti* were not recorded, but subsequent observations on the Kenya coast have shown that var. *queenslandensis* (the "pale form") is mainly house-haunting, and ssp. *formosus* (the "dark form") is usually confined to outside situations. It is considered probable that the examples of *Aë. aegypti* taken in the house catches were mainly of var. *queenslandensis* and those in the bush of ssp. *formosus*. The difference in the biting cycles of *Aë. aegypti* for bush and house supports this hypothesis.

C. p. fatigans (fig. 4, c).—Though a few individuals were observed biting during the day, this subspecies was mainly nocturnal and the majority was taken in house catches. The seasonal incidence was similar inside and outside but too few were taken in the bush to show a definite pattern. May was the most productive month, but *C. p. fatigans* also occurred in relatively high numbers in the last four months of the year. The biting curve showed three waves of activity with an initial low peak just after sunset; most biting took place in the second half of the night. In the house, the main biting began in the hour before midnight and continued until 02 hr. In the bush, the main peak was between 03 and 05 hr., and in the compound there was a sharp rise between midnight and 01 hr.

While the biting cycle for the above three species was very similar in the three situations, the time and magnitude of the main biting peaks varied. At the present stage in our knowledge no explanation can be given for these differences, but Haddow (1954) suggests that mosquitos are "released" for biting by favourable conditions and that the biting pattern is related to separate, though as yet unknown, groups in the female population. If this is so, the difference shown here in the biting rhythms, inside and outside, might be explained by a particular female group favouring a certain environment for feeding.

Species biting in the bush.

Seven species were taken of which the biting activity was almost entirely restricted to the bush; the biting cycles are shown in fig. 5.

Anopheles squamosus Theo. (fig. 5, g) was almost entirely nocturnal and the biting cycle showed an initial rise after sunset with a peak in the next hour; the main biting took place between midnight and 05 hr. It only rarely entered houses to bite between 21 and 06 hr. and five of the seven mosquitos taken bit between midnight and 06 hr. In the compound, a total of nine examples of *A. squamosus* was taken between midnight and 05 hr.

Taeniorhynchus africanus (fig. 5, e) was nocturnal, though a few came to the bait during the day. At Ganda and Mambrui there were two waves of activity with the main biting peak between 02 and 06 hr. and another lower peak after sunset from 18 to 22 hr. This picture is rather different from that previously

recorded for *T. africanus* by Haddow (1945), Haddow, Gillett & Highton (1947) and Mattingly (1949*a*) where the main biting was during the first half of the night. Thirty two examples of *T. africanus* were caught biting inside during the night hours and, of these, 20 came between 03 and 05 hr.; one was taken in the compound between 22 and 23 hr.

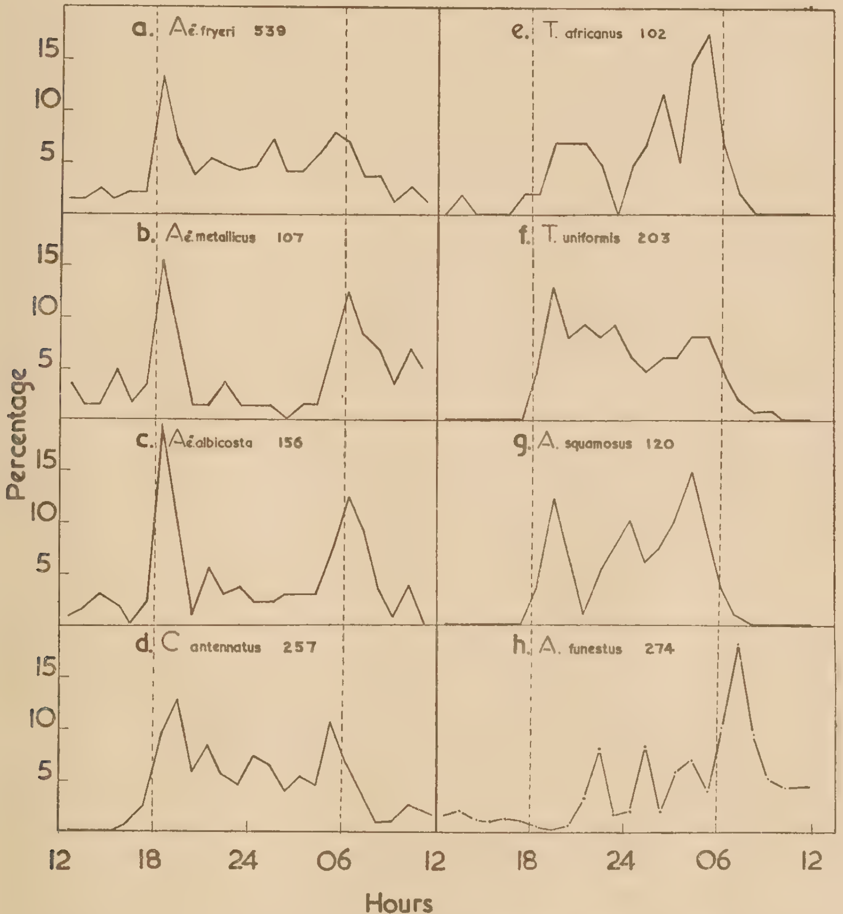

Fig. 5.—a–g, biting cycles of seven bush-frequenting species as shown by geometric means reduced to percentages; h, one 24-hr. catch of *A. funestus* taken indoors, hourly figures expressed as percentage of total catch.

Taeniorhynchus uniformis (fig. 5, f) was nocturnal and the biting cycle agrees closely with that previously recorded for this species (Haddow, 1945). It had a peak of activity after sunset in the period 18 to 22 hr., after which the biting remained high, though not reaching the same level as in the peak period. Sixty two examples of *T. uniformis* were taken inside, all during the hours of darkness, and the biting peak was between 22 and 24 hr.; 22 were taken in this period. Nineteen were taken biting in the compound. Although most of these were

TABLE V.

Rare species in 24-hour catches.

	Anopheles (Anopheles) coustani Lav.	*Culex (Culex) perfuscus* Edw.	*Aëdes (Skusea) pembaensis* (Theo.)	*Anopheles (Anopheles) coustani tenebrosus* Dön.	*Aëdes (Stegomyia) simpsoni* (Theo.)	*Aëdes (Mucidus) scatophagoides* (Theo.)	*Aëdes (Diceromyia) adersi* (Edw.)	*Anopheles (Myzomyia) pharoensis* Theo.	*Aëdes (Dunnius) michaelikati* van Som.	*Aëdes (Banksinella) albothorax* (Theo.)	*Anopheles (Anopheles) coustani ziemanni* Grünb.	*Culex (Culex) annulioris* Theo.	*Aëdes (Stegomyia) calceatus* Edw.	*Aëdes (Aëdimorphus) tarsalis* (Newst.)	*Aëdes (Aëdimorphus) cumminsi mediopunctatus* (Theo.)	*Aëdes (Aëdimorphus) ochraceus* (Theo.)	*Aëdes (Diceromyia) taylori* (Edw.) or *Aë. (D.) furcifer* (Edw.)	*Eretmapodites quinquevittatus* Theo.	*Aëdes (Stegomyia) soleatus* Edw.	*Aëdes (Finlaya) fulgens* (Edw.)	*Aëdes (Mucidus) mucidus* (Karsch)
Compound ..	1	1	2																		
House ..	3	4		2	1	1	1														
Bush ..	24	18	30	4	59	29	10	16	5	5	4	4	4	3	3	3	3	1	1	1	1
Sunset ..	+	+	+	+	+		+	+	+	+		+	+		+		+			+	
Darkness ..	+	+	+	+	+	+	+	+	+	+	+	+					+				+
Dawn ..	+	+	+		+	+		+			+			+	+	+	+		+		
Daylight ..			+		+				+				+					+			

taken at night, two were caught in daylight between 06 and 07 and 13 and 14 hr., respectively; 11 of the 19 examples bit after midnight between 24 and 04 hr.

Aëdes fryeri (fig. 5, a) was mainly nocturnal, though biting occurred throughout the day. The cycle showed two clear peaks about sunset and dawn; the evening peak occurred between 18 and 19 hr. and was higher than the morning peak which was of longer duration and spread over the period from 05 to 07 hr. This agrees closely with the biting cycle given by Lumsden (1955) for *Aë. fryeri* in *Avicennia* forest in the Gede area. No examples of *Aë. fryeri* were taken inside and only one in the compound.

Aëdes metallicus (Edw.) (fig. 5, b) showed two main peaks of activity. There was a pronounced peak after sunset between 18 and 19 hr., after which biting dropped sharply and remained at a low level throughout the night; biting increased again about dawn and there was a peak between 06 and 07 hr. Only one example of *Aë. metallicus* was taken inside, between 17 and 18 hr., and six were taken in the compound, four in the first half of the morning and two between 22 and 24 hr.

Aëdes albicosta (fig. 5, c). Here again there was a definite morning and evening peak and the cycle was very similar to that of *Aë. metallicus*. No examples were taken in the compound and only one in the house, between 07 and 08 hr.

Culex antennatus (Becker) (fig. 5, d) was mainly nocturnal with the initial biting before sunset and a peak between 19 and 20 hr.; thereafter the biting dropped but remained at a high level throughout the night; there was another peak in the hour before dawn. One individual of *C. antennatus* was taken inside just after sunset and 175 were taken in the compound in one catch only. In the compound, the biting occurred between 23 and 07 hr. and 142 were taken between 03 and 06 hr. The figures are as follows:—23–24 hr. (1), 24–01 hr. (5), 01–02 hr. (12), 02–03 hr. (5), 03–04 hr. (50), 04–05 hr. (24), 05–06 hr. (68), 06–07 hr. (10).

Rare species.

The remaining species were taken in small numbers, and although most of them were very rare, 274 examples of *A. funestus* were taken in a single catch in the rented house in December 1951. The figures for this catch are plotted in fig. 5, h. They show that *A. funestus* was inactive in the sunset period and biting was at a minimum between 12 and 21 hr. Biting increased in the latter part of the night and was irregular until dawn, after which there was a sharp peak between 06 and 08 hr.

The other species are recorded in Table V. As the numbers are small the 24 hours are divided into four arbitrary periods called "dawn" (05–08 hr.), "daylight" (08–17 hr.), "sunset" (17–20 hr.) and "darkness" (20–05 hr.) and the species are recorded as they occur in each of these periods in bush catches only. The actual numbers for *Aë. pembaensis* (Theo.) and *Aë. simpsoni* (Theo.) show biting cycles very similar to those already recorded for these two species by Lumsden (1955). *Aë. pembaensis* was taken biting throughout the day and night but most came to bait in the hours of darkness; 21·9 per cent. of the total catch was taken between 18 and 19 hr., which was the peak period recorded by Lumsden for his catches in *Adansonia* bush in the Gede area. Forty nine of the 59 examples of *Aë. simpsoni* taken were biting during daylight between 06 and 18 hr. The hourly figures showed a lull in activity between 12 and 14 hr. and a higher morning than afternoon peak. This is much the same as the cycle recorded by Lumsden for *Aë. simpsoni* in forest, except that his cycle showed a higher afternoon than morning peak.

With the exception of *C. p. fatigans*, all the species shown in Table VI are prevalent in the bush in the second quarter of the year, during the main rainy

season, when biting in houses is at a minimum. In the second half of the year, when there are high winds, there is a greater tendency for mosquitos to bite in houses.

TABLE VI.

Seasonal incidence of biting mosquitos, Ganda and Mambrui (arithmetic totals).

	Months	J	F	M	A	M	J	J	A	S	O	N	D
Aë. aegypti	House ..	10	18	13	111	73	6	27	3	8	8	12	21
	Bush ..	1	2	11	36	11	13	6	1	–	6	–	11
	*Totals ..	11	32	31	189	126	32	43	8	8	15	13	47
C. p. fatigans	House ..	15	8	16	41	81	5	17	11	63	44	34	41
	Bush ..	1	5	4	9	3	3	4	3	5	10	4	12
	*Totals ..	16	27	23	72	110	9	22	18	70	56	39	54
C. sitiens	House ..	1	–	–	480	51	96	59	134	11	1	1	–
	Bush ..	2	–	4	216	610	844	425	648	199	13	11	5
	*Totals ..	3	–	4	902	750	978	528	805	218	14	12	5
T. uniformis	House ..	–	–	–	–	2	1	4	8	–	–	2	45
	Bush ..	–	–	–	27	49	2	47	29	1	1	19	1
	*Totals ..	–	–	–	28	53	3	56	40	1	1	26	49
T. africanus	House ..	–	–	–	–	–	–	–	–	–	–	–	32
	Bush ..	–	–	–	70	2	–	5	–	1	–	6	1
	*Totals ..	–	–	–	71	2	–	5	–	1	–	6	33
A. gambiae	House ..	–	–	–	42	10	10	33	67	10	–	–	–
	Bush ..	1	–	–	21	67	47	4	49	25	2	1	3
	*Totals ..	1	–	–	106	102	65	41	206	46	4	1	3
Totals	*A. squamosus*	–	–	–	12	107	–	26	–	–	–	–	–
	Aë. metallicus	1	1	–	39	46	7	5	–	–	–	3	2
	C. antennatus	–	–	–	6	438	–	16	–	–	–	–	–
	Aë. fryeri ..	–	2	3	241	201	4	33	1	–	–	–	75
	Aë. albicosta	–	3	–	102	39	12	4	–	–	–	2	–

* Including catches in the compound.

Summary.

The mosquitos of two villages on the Kenya coast were studied over a period of two and a half years, which included years of very light, average and very heavy rainfall. A survey was made of the species occurring in the bush and in the houses, and in addition 24-hour biting catches were done and window-trap

catches were examined to obtain information on the movement of species in and out of houses.

Sixty five species were taken in net catches in the bush but only 19 were taken regularly; five (*Taeniorhynchus uniformis* (Theo.) and *T. africanus* (Theo.), *Aëdes woodi* Edw., *Culex invidiosus* Theo. and *C. guiarti* Blanch.) were abundant. In the houses, two species, *C. pipiens fatigans* Wied. and *Aë. aegypti* occurred regularly, the former being abundant and the latter not uncommon. *Anopheles gambiae* Giles and *A. funestus* Giles were seasonal; *A. funestus* appeared only after exceptionally heavy rain. The in-going window trap attracted only an occasional mosquito seeking shelter during the day and only six species were taken. Thirty species were found in the out-going trap but only seven occurred regularly. *A. gambiae*, *A. funestus*, *T. uniformis*, *T. africanus* and *C. p. fatigans* were most active during the hours of darkness, with the main activity in the four hours before dawn. *Aë. aegypti* had two waves of activity, in the four-hour periods before dawn and before sunset, respectively; the sunset peak was higher and the main activity probably occurred between 18 and 19 hr., as previously recorded for this species in Mombasa.

Thirty five species were taken biting in the 24-hour catches in situations designated bush, house and compound, respectively. The biting cycles of *A. gambiae*, *Aë. aegypti* and *C. p. fatigans* have been compared in the three situations. The biting rhythm of each species was much the same in the different environments but the time and magnitude of the main peaks varied. In the case of *Aë. aegypti*, which probably includes two different forms, there is a marked difference in the magnitude of the evening peak in the bush and house. The biting cycles in the bush are given for *A. squamosus* Theo., *T. uniformis*, *T. africanus*, *Aë. fryeri*, *Aë. metallicus* (Edw.), *Aë. albicosta* (Edw.) and *C. antennatus* (Becker) and their occurrence in the other two situations is noted. The cycles of *T. uniformis* and *Aë. fryeri* agree with previous findings, but that of *T. africanus* differs from other cycles recorded for this species by having the main biting after midnight. The remaining species were rare, but one catch of 274 specimens of *A. funestus* was recorded.

Resting mosquitos were more numerous in the second half of the year from August to December, a period of light rainfall and high temperatures. Biting mosquitos were more commonly taken, especially in the bush, in the second quarter of the year, during the main rainy season. The biting activity of some species increased in the houses in the second half of the year, when there are high winds, and biting in the bush was minimal.

Acknowledgements.

We wish to thank Mr. A. E. C. Harvey for help in the calculations, Mr. Goiny for the maps and Messrs. Guggisberg and McPhee for the figures.

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ACARICIDE RESISTANCE IN THE BLUE TICK, *BOOPHILUS DECOLORATUS* (KOCH).—PART I.

By G. B. Whitehead

(Plate XXVI.)

The Blue Tick, *Boophilus decoloratus* (Koch), from the eastern coastal areas of South Africa was shown in 1940 to be resistant to sodium-arsenite dipping preparations (Du Toit, Graf & Bekker, 1941). Previous to this, sodium-arsenite dips had been effectively used for 30 to 40 years. Arsenic resistance in the Blue Tick occurred only in ticks from a narrow coastal belt stretching from Port Elizabeth in the south through Natal in the north.

BHC preparations replaced sodium arsenite in areas affected by the arsenic-resistant tick but after 18 months the first instances of BHC resistance were detected (Whitnall & Bradford, 1949). The BHC-resistant tick in a short time covered the same area originally covered by the arsenic-resistant tick. At that time, from many hundreds of tests, no instance was found where the BHC-resistant tick was not also resistant to arsenic (Whitnall & others, 1952). Resistance to both arsenic and BHC, although initially confined to the coastal areas, has been recently observed in the Blue Tick in localised areas of the Transvaal, East Africa (Dr. H. S. Purchase, personal communication) and in Northern Rhodesia (Matthysse, 1954). In most of these areas, arsenic and BHC resistance appear to occur together and this is suggestive of a cross-resistance. This, however, is not the case, as arsenic resistance developed first, and at that stage, arsenic-resistant ticks were sensitive to BHC. It has been shown in some areas that the Blue Tick has developed resistance to BHC without prior resistance to sodium arsenite (Bekker, 1953).

For six years, DDT remained effective against the tick that was resistant to both arsenic and BHC but the first instances of DDT resistance were detected on isolated farms in the East London area during 1954 (Whitehead, 1956). DDT-resistant ticks were also resistant to arsenic and BHC. Resistance to all three of these chemicals developed independently, suggesting that the mechanisms of resistance are unrelated.

This paper covers the experimental work undertaken to determine quantitatively the resistance of the Blue Tick to a variety of insecticides * and where possible to relate the different types of resistance.

Methods.

Tests were conducted with both fully engorged adult female ticks and with unfed newly hatched larvae. In determining the response of both adult and larval ticks to insecticides, it was necessary to obtain a standard population against which strains of unknown tolerance could be compared. For this purpose it would have been most desirable to use ticks from an area where no insecticide had ever been used. This, however, was not possible and ticks from Frankenwald Experimental Farm, on the outskirts of Johannesburg, were used as a standard of comparison. Both BHC and toxaphene dipping preparations had been used at Frankenwald for the field control of ticks but no signs of increased tolerance

* In view of the fact that all the substances tested were originally developed as insecticides, this term has been used throughout the paper in preference to "acaricide".

to these materials in the field had been observed. For the purpose of this work, ticks from Frankenwald were regarded as sensitive to all insecticides.

Breeding of ticks.

Sensitive ticks were either collected at random from range cattle at Frankenwald or from selected animals that were artificially infested with larvae originally obtained from Frankenwald range cattle. Resistant ticks were obtained from two farms, Ferndale and Allandale, located in the East London district and despatched by air to the laboratory.

In tests employing adult ticks, the fully engorged females were used 3–5 days after removal from the host. For a supply of larvae, female ticks were placed in glass tubes loosely stoppered with cotton-wool and stored at 25°C. and at a relative humidity of 80 per cent. In order to minimise the possibility of selecting larvae from a single parent, between 10 and 20 fully engorged females were placed in each breeding tube. On hatching, the larvae soon became thoroughly mixed. Larvae used in tests were all between 15 and 30 days old.

Tests using the adult female tick.

The biological test using the fully engorged female Blue Tick is an adaptation of that described by Whitnall & Bradford (1947). Fully engorged female ticks were dipped in a range of concentrations of wettable-powder preparations of insecticide in an immersion apparatus (Pl. XXVI, fig. 1). The apparatus, which is an adaptation of an instrument originally described by McIntosh (1947). consists of a constant-temperature water bath containing a rotating end-over-end shaker in which a glass tube may be clamped. The bath was maintained at 25°C. and the shaker rotated at 32 r.p.m.

Batches of 50 adult ticks, selected for uniformity of engorgement, were placed in glass tubes measuring 1 × 3 inches. The appropriate concentration of insecticide suspension, preconditioned to 25°C., was poured over the ticks, the tube well stoppered and rotated in the immersion apparatus for two minutes. After immersion, the contents of the tube were poured into a petri dish and the ticks immediately removed with forceps and placed on pads of cotton-wool moistened with the same insecticide concentration as that used for dipping. Treated ticks were allowed to drain in this manner for half an hour and were then placed in conveniently sized glass tubes which were loosely stoppered with cotton-wool. Control batches treated with water alone were included in all tests. If more than 5 per cent. mortality occurred in the control batches the entire test was discarded. Tubes containing treated ticks were stored in trays at 25°C. and a relative humidity of 80 per cent. A record was kept of the number of ticks that laid eggs, size of egg batches and the percentage hatch. Treatment with some insecticides did not result in an outright kill of adult female ticks but achieved control by affecting the viability of the eggs produced. For this reason, final results were expressed as a percentage control. In instances where the insecticide acted directly on the adult tick; percentage control is the same as percentage kill.

Tests using unfed larvae.

Batches of larvae were dipped in wettable-powder suspensions of insecticide in the same apparatus as that used for adult ticks. For convenience, smaller dipping tubes measuring $\frac{3}{4}$ × 2 inches were used. Larvae were removed from breeding tubes in batches of between 100 and 200 with a small camel-hair brush and deposited in the dipping tubes. Approximately 10 ml. of the appropriate insecticide concentration was then added, the tube stoppered, placed in the immersion apparatus and rotated at 32 r.p.m. for one minute.

After immersion, larvae were separated from the insecticide suspension by

pouring the contents of the dipping tube through a separating apparatus (Pl. XXVI, fig. 2). The separating apparatus comprised two flanged glass cylinders approximately 1½ inches in diameter placed one above the other. A circular disc of 40-mesh copper gauze with a thin rubber washer was placed between the faces of the two flanges and the two clamped together with spring clips. The apparatus was conveniently used on a filter flask as recovery vessel although the application of vacuum had no advantage.

After pouring the insecticide, together with the larvae, through the separating apparatus, the tube was rinsed with 10 ml. distilled water to remove any larvae remaining in it. The batch of larvae retained by the copper gauze was then washed with a further 10 ml. distilled water.

After washing, the copper gauze disc was removed and dried by contacting the under surface with absorbent paper. The gauze discs, still retaining the treated larvae, were placed in paper envelopes and sealed by crimping the edges between a set of serrated rollers (Pl. XXVI, fig. 3). Envelopes were made of a high quality glazed paper (Pl. XXVI, fig. 4) and were kept for at least 24 hours at 25°C. and 80 per cent. R.H. before use to allow the paper to come to equilibrium with the high atmospheric humidity. Filter-paper envelopes, although most convenient, were not satisfactory for all strains of ticks as they resulted in a high mortality in the water-treated controls, presumably as a result of a dehydration effect. The effect was particularly marked with sensitive larvae. In the construction of glazed-paper envelopes, use was made of both a mucilage application and mechanical crimping as neither crimping nor mucilage application alone gave a satisfactory seal under conditions of high humidity.

All operations in the test procedure were carried out in a constant-conditions

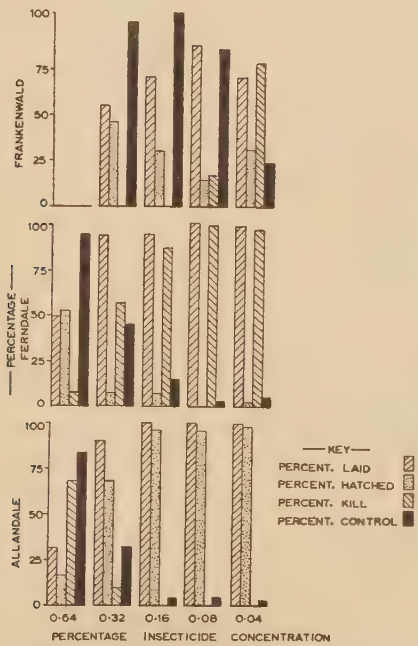

Fig. 1.—The effect of sodium arsenite on adult females of *B. decoloratus*.

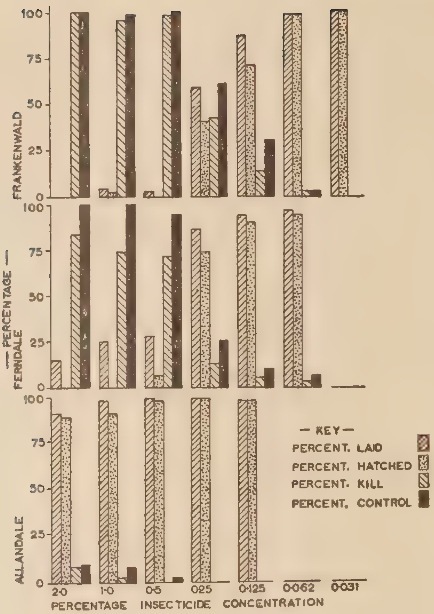

Fig. 2.—The effect of p,p′DDT on adult females of *B. decoloratus*.

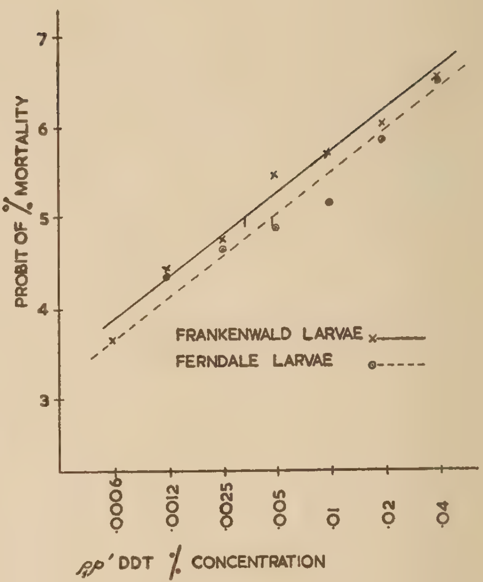

Fig. 3.—The effect of p,p′DDT on larvae of *B. decoloratus*.

LC50 for Frankenwald larvae, 0·0049%, standard deviation 0·000625: LC50 for Ferndale larvae, 0·0034%, standard deviation 0·000313. Difference in response is not significant.

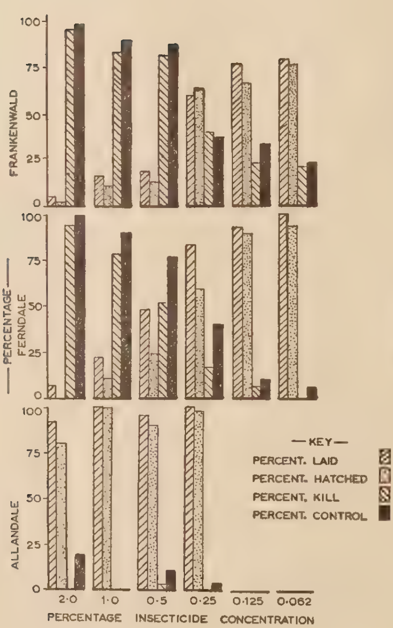

Fig. 4.—The effect of Dilan on adult females of *B. decoloratus*.

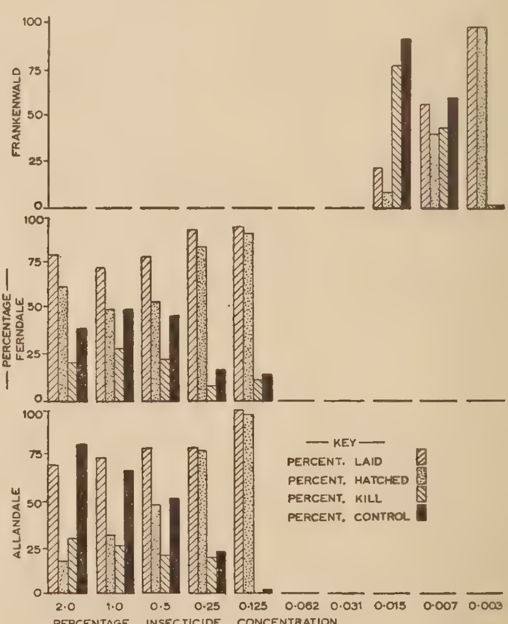

Fig. 5.—The effect of γ BHC on adult females of *B. decoloratus*.

room at 25°C. and 80 per cent. R.H. Mortality counts were made 24 hours after exposure. The criterion of mortality was taken as an absence of any movement in larvae when the envelope was opened.

Tests with each insecticide concentration were replicated five times, giving a total of between 700 and 1,000 larvae per insecticide concentration. A water-treated control was included with all tests, and in any tests where mortality in the control was more than 5 per cent. the entire series was discarded. Results of tests were analysed by the method of probits from which the concentration of insecticide required to produce 50 per cent. kill (LC50) was determined, if necessary by extrapolation.

Results.

Sodium arsenite.

The effect of sodium-arsenite preparations on sensitive and resistant adult ticks may be compared in the following histogram (fig. 1). One hundred per cent. control was achieved with 0·16 per cent. As_2O_3 on Frankenwald ticks but less than 20 per cent. control with ticks from both the farms Ferndale and Allandale. Concentrations of 0·64 per cent. As_2O_3 resulted in over 80 per cent. control of arsenic-resistant strains and at this concentration there is little doubt that sodium arsenite would be effective for the field control of the arsenic-resistant Blue Tick. Because of mammalian toxicity, however, the use of high concentrations of arsenic is not practicable.

A comparison of these results (fig. 1), which were obtained in 1956, with those obtained by Whitnall & Bradford (1947) using an identical technique, shows that the degree of arsenic tolerance in resistant strains of the Blue Tick has not changed in ten years. Resistant strains appear to have maintained a 3- to 4-fold increase in tolerance in spite of the fact that dipping in sodium-arsenite preparations had not been practised during that time.

It is of interest to note that *Boophilus microplus* (Can.) from Australia is remarkably similar to *B. decoloratus* from South Africa in response to arsenic in both sensitive and resistant strains. Results of the toxicity of sodium arsenite to *B. microplus* (Hitchcock, 1953) and *B. decoloratus* obtained using the same test procedure may be compared in Table I.

TABLE I.

Comparison of the effect of sodium arsenite on Australian and South African species of *Boophilus*.

Sodium arsenite (0·04% As_2O_3)	Percentage control	
	Resistant strain	Sensitive strain
B. microplus (Australia) ..	4	25
B. decoloratus (South Africa) ..	5	24

Unfortunately, the effect of sodium arsenite on larvae of the Blue Tick could not be assessed as the test procedure used with wettable-powder preparations was not satisfactory with sodium-arsenite solutions.

DDT.

Adult ticks from the farm Allandale (fig. 2) were considerably more tolerant of DDT than were ticks from Ferndale and Frankenwald. There appeared to be a slight difference in response to DDT in adult ticks from Ferndale and Frankenwald but this difference could not be demonstrated with larvae (fig. 3).

Dilan.

Dilan, a mixture of 2-nitro-1,1-bis(p-chlorophenyl)propane and 2-nitro-1,1-bis(p-chlorophenyl)butane, was as effective against Frankenwald adult ticks as it was against Ferndale ticks but was completely ineffective against the DDT-resistant Allandale tick (fig. 4). Dilan appeared as effective against both Frankenwald and Ferndale ticks as did DDT (figs. 2 & 4). The Allandale tick was approximately as resistant to Dilan as it was to DDT, indicating a cross-tolerance between DDT and Dilan in Allandale ticks.

No tests with Dilan using larval ticks were undertaken as wettable-powder formulations of Dilan were not available.

BHC, toxaphene, chlordane, dieldrin and aldrin (figs. 5–14).

When compared with Frankenwald ticks, Ferndale adult and larval ticks and Allandale adult ticks were all highly tolerant to the above group of insecticides. When BHC resistance was first noted it was observed that BHC-resistant ticks showed an increased tolerance to toxaphene which had not been used commercially at that time (Whitnall & others, 1952). Chlordane, dieldrin and aldrin have never been used commercially for the control of the Blue Tick in South Africa and resistance to these materials is clearly a result of a cross-tolerance conferred by resistance to BHC.

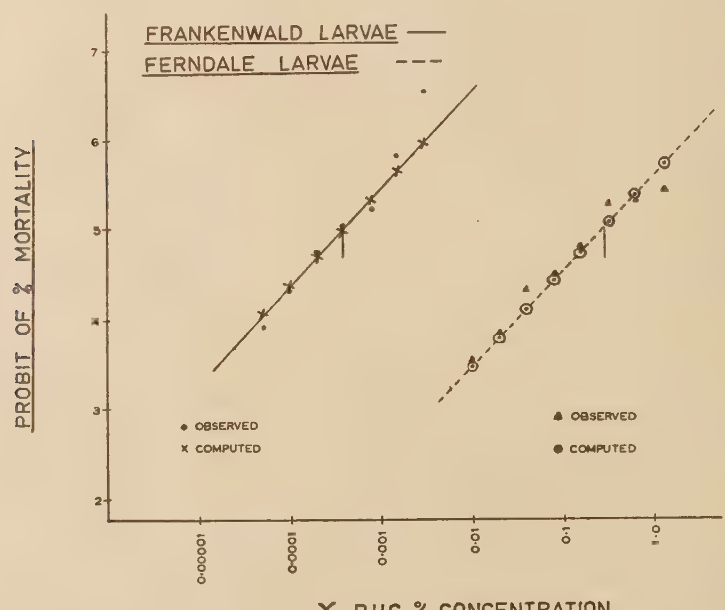

Fig. 6.—The effect of γ BHC on larvae of *B. decoloratus*. LC50 for Frankenwald larvae, 0·0002%, standard deviation, 0·0000034: LC50 for Ferndale larvae, 0·2395%, standard deviation, 0·00500. Difference in response is highly significant.

BHC resistance for many years occurred only in ticks from the eastern coastal belt of South Africa where all BHC-resistant ticks were also resistant to arsenic. More recently, a strain of Blue Tick resistant to BHC but not to arsenic was shown to have developed on a farm near Pretoria (Bekker, 1953). Results of laboratory tests on adult female ticks from Sandown, on the outskirts of Johannesburg, are presented in Table II.

TABLE II.

Effect of BHC and sodium arsenite on adult ticks from Sandown and Frankenwald.

Percentage insecticide concentration	Percentage control	
	Sandown ticks	Frankenwald ticks
BHC (0·01%)	0	100
Sodium arsenite (0·16% AS_2O_3)	90	90
Water-treated control ..	0	0

These results confirm the existence of a BHC-resistant, arsenic-sensitive Blue Tick in the interior districts of South Africa.

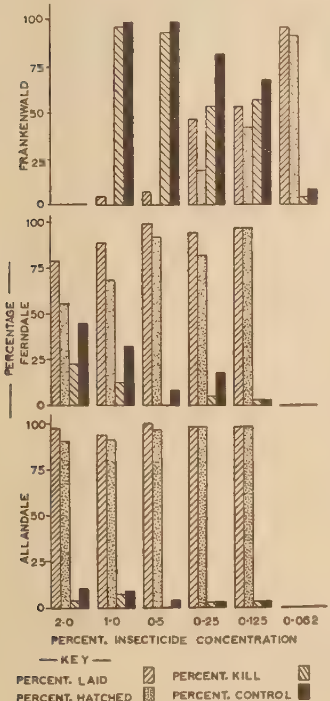

Fig. 7.—The effect of toxaphene on adult females of *B. decoloratus*.

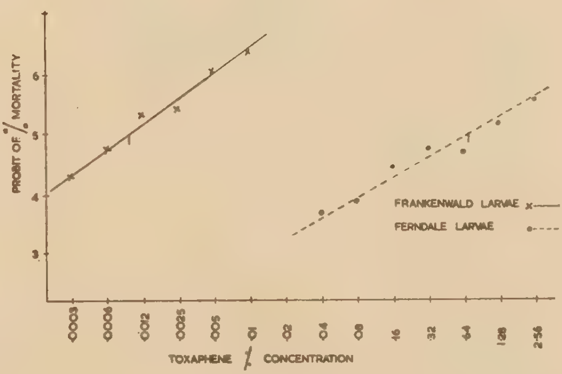

Fig. 8.—The effect of toxaphene on larvae of *B. decoloratus*.
LC50 for Frankenwald larvae, 0·000870%, standard deviation, 0·000156: LC50 for Ferndale larvae, 0·8292%, standard deviation, 0·020. Difference in response is highly significant.

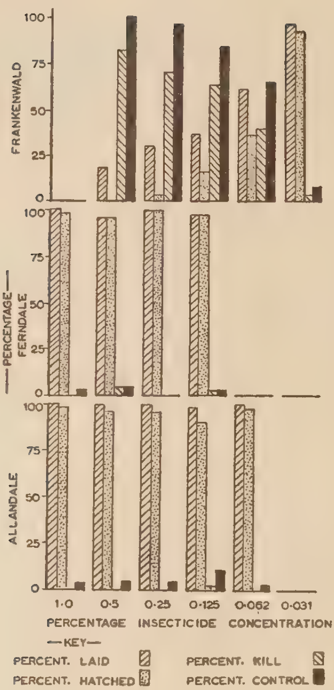

Fig. 9.—The effect of chlordane on adult females of *B. decoloratus.*

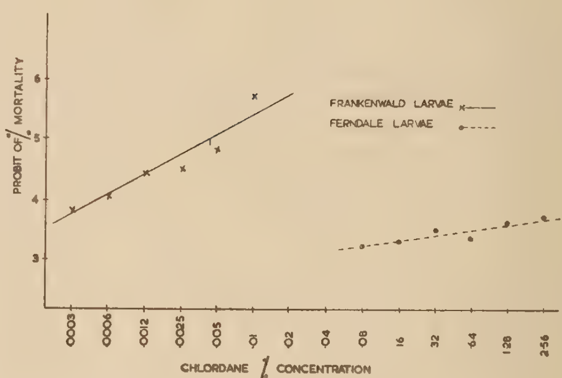

Fig. 10.—The effect of chlordane on larvae of *B. decoloratus.*

LC50 for Frankenwald larvae, 0·0042%, standard deviation, 0·000156: LC50 for Ferndale larvae, 30156%, standard deviation, 0·0423. Difference in response is highly significant.

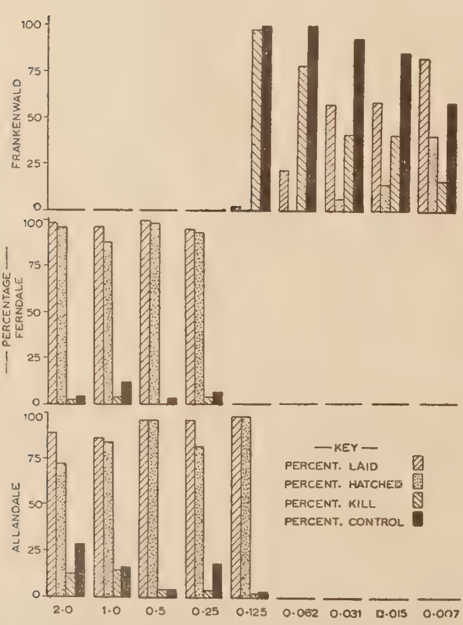

Fig. 11.—The effect of dieldrin on adult females of *B. decoloratus.*

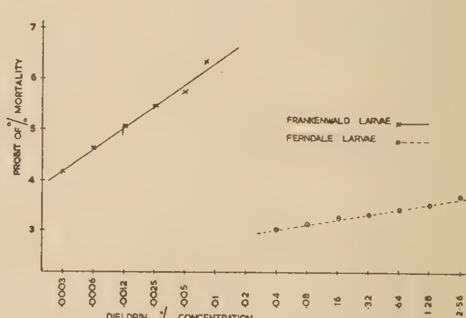

Fig. 12.—The effect of dieldrin on larvae of *B. decoloratus.*

LC50 for Frankenwald larvae, 0·0012%, standard deviation, 0·000156: LC50 for Ferndale larvae, 26971·0%. Difference in response is highly significant.

Malathion and diazinon.

Adult and larval ticks from Frankenwald, Ferndale and adults from Allandale were all approximately equally affected by both diazinon and malathion. There was no apparent cross-tolerance to these organo-phosphorus insecticides resulting from a resistance to any other non-organo-phosphorus insecticide. These results

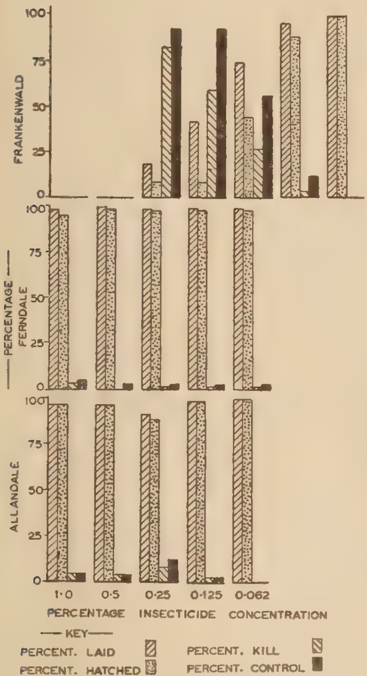

Fig. 13.—The effect of aldrin on adult females of *B. decoloratus.*

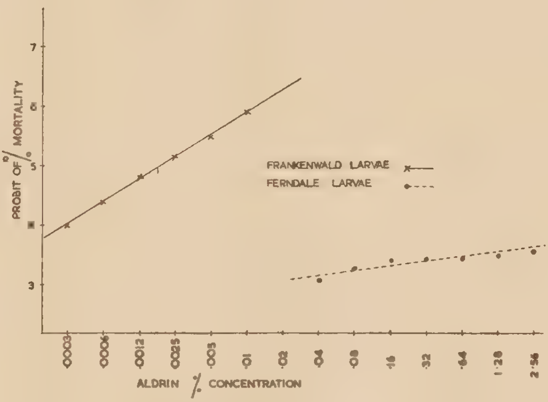

Fig. 14.—The effect of aldrin on larvae of *B. decoloratus.*
LC50 for Frankenwald larvae, 0·0017%, standard deviation, 0·000156: LC50 for Ferndale larvae, 71031·0%, standard deviation, 0·0216. Difference in response is highly significant.

are at variance with those obtained by Fiedler (1952) where arsenic and BHC resistance apparently conferred some cross-resistance to the organo-phosphorus compound, parathion.

Discussion.

Comparative effectiveness of a number of insecticides on Boophilus decoloratus.

The concentration of insecticide required to produce 50 per cent. mortality of both Frankenwald (sensitive) and Ferndale (resistant) larvae, obtained with the larval test procedure already described, is presented in Table III.

Of the insecticides investigated for effectiveness on Frankenwald larvae, γ BHC produced 50 per cent. mortality at the lowest concentration. Following in order of decreasing effectiveness were toxaphene, dieldrin, aldrin, chlordane, DDT and malathion. In respect of the adult fully engorged female tick the test employed was not sufficiently sensitive to give a precise measure of effectiveness of an insecticide. The range of insecticides used could, however, be placed in an

approximate order of effectiveness gauged by the concentration of insecticide used to produce complete control. The order of effectiveness of the insecticides used on adult fully engorged female ticks from Frankenwald was (1) γ BHC, (2) chlordane, toxaphene, Dilan and DDT, (3) dieldrin, (4) sodium arsenite, (5) aldrin, (6) malathion.

TABLE III.

The percentage concentration of insecticide required to produce 50 per cent. mortality of tick larvae from Frankenwald and Ferndale.

Insecticide	LC50		
	Frankenwald larvae	Ferndale larvae	Factor of increased tolerance
p,p'DDT ..	0·0049	0·0034	—
γ BHC ..	0·0002	0·2395	8×10^2
Chlordane ..	0·0042	30156·0 *	7×10^6
Toxaphene ..	0·0008	0·8292	9×10^2
Dieldrin ..	0·0012	26971·0 *	2×10^7
Aldrin ..	0·0017	71013·0 *	3×10^7
Malathion ..	0·1034	0·0819	—

* Computed from results obtained with the highest concentrations used.

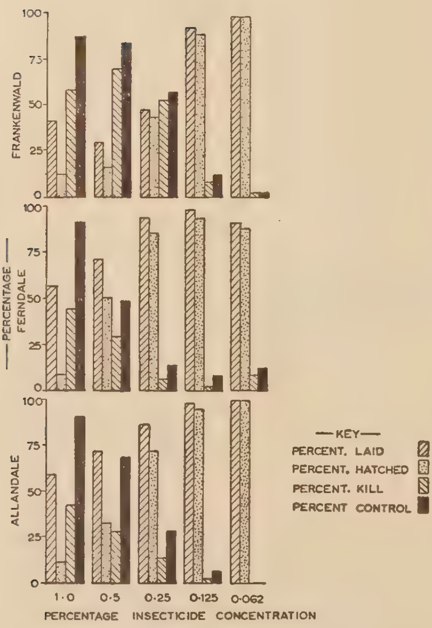

Fig. 15.—The effect of malathion on adult females of *B. decoloratus*.

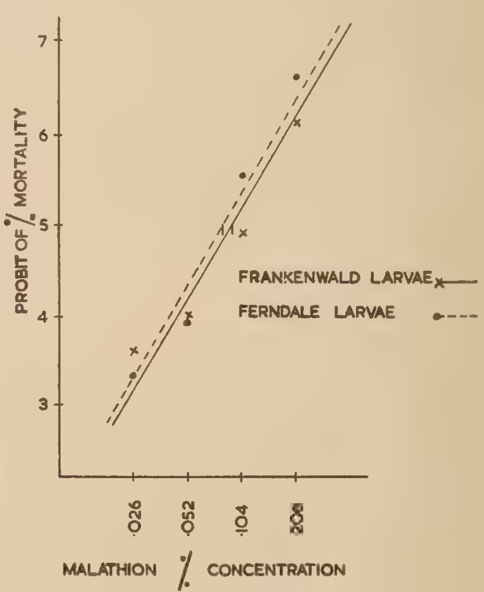

Fig. 16.—The effect of malathion on larvae of *B. decoloratus*.

LC50 for Frankenwald larvae, 0·1034%, standard deviation, 0·0130: LC50 for Ferndale larvae, 0·0819%, standard deviation, 0·0130. Difference in response is not significant.

Relationships in resistance to insecticides in Boophilus decoloratus.

From the results obtained in the above tests, together with the accumulated historical evidence in the development of resistance to insecticides in the Blue Tick, three distinct types of resistance appear to exist, namely, resistance to (a) arsenic, (b) γ BHC, automatically conferring a cross-tolerance to toxaphene, chlordane, dieldrin and aldrin and (c) DDT, automatically conferring a cross-tolerance to Dilan. Each type of resistance has developed independently and could occur separately or together in any single population of ticks.

Cross-resistance to insecticides in the Blue Tick is similar to that found in the house-fly, *Musca domestica* L. (Busvine & Harrison, 1953) and it might be inferred that the mechanisms of resistance are similar. DDT resistance, however, appears to be an exception in that it shows a cross-tolerance to Dilan which is not the case in certain Diptera (Metcalf, 1955). This evidence suggests that dehydrochlorination of DDT may not be a contributing factor in DDT resistance in the Blue Tick. This is supported by the findings in DDT-resistant *B. microplus* where the DDT-dehydrochlorinase enzyme found by Sternburg, Kearns & Moorefield (1954) in house-flies was not present (W. J. Roulston, unpublished abstract from W.H.O. Information Circular on the Resistance Problem, no. 5, 1957).

Distribution of resistant strains of Boophilus decoloratus.

The distribution, in South Africa, of populations of the Blue Tick resistant to insecticides suggests that climatic conditions play some part in the development of resistant tick populations.

The eastern coastal area enjoys an equable climate with a frost-free winter. Inland areas differ in that the winters are severe with several months of frost and excessively low humidities. The Blue Tick, along the coast, although most abundant during the summer, will continue to breed throughout the winter. Inland, it is numerous only during the summer and even in this season never assumes the high populations common along the coast.

Rapid development of tick populations along the coast has necessitated the dipping of cattle at seven-day intervals during the summer and at 14-day intervals during the winter. Rapid breeding and the consequent frequent treatment with insecticide had undoubtedly contributed greatly to the development of the various types of resistance to insecticides now manifest in the Blue Tick from coastal areas. These facts suggest that resistance to insecticides would develop in the Blue Tick from the interior districts of South Africa provided a sufficient number of generations were repeatedly treated with a specific insecticide. This, in fact, has been the case in respect of BHC resistance which has developed in the Transvaal, but only after five or six years of the field use of BHC as compared with the coastal area where BHC resistance developed 18 months after first being used. Development of any resistance to insecticides in inland areas may be only a question of time.

Summary.

Using laboratory tests described, the effectiveness of a number of insecticides on both larval and adult, fully engorged examples of the Blue Tick, *Boophilus decoloratus* (Koch), was determined. The results of tests using adult ticks were expressed as histograms of the percentage control exerted by varying concentrations of insecticides. The test using larvae was more sensitive and enabled results to be expressed as dose-response curves from which the LC50 could be accurately calculated. By comparing ticks from different localities in South Africa, resistance to a number of insecticides was demonstrated. Adult ticks from the farms Allandale and Ferndale in the East London district were three to four times more tolerant of sodium arsenite than were the sensitive ticks from

Frankenwald farm near Johannesburg. Both larval and adult ticks from Ferndale and Allandale, when compared with Frankenwald ticks, were highly resistant to γ BHC, which conferred some cross-resistance to toxaphene, chlordane, dieldrin and aldrin. Ticks from Allandale, in addition to being resistant to sodium arsenite, BHC, toxaphene, chlordane, dieldrin and aldrin were highly resistant to DDT. DDT resistance conferred a cross-resistance to Dilan.

The organo-phosphorus insecticides tested, malathion and diazinon, were equally effective against all ticks.

Acknowledgements.

The work described in this communication was carried out at the Research Department of Messrs. African Explosives & Chemical Industries, Ltd., to whom thanks are due for permission to publish the results. Much of the field collection of tick specimens was carried out by Dr. W. M. McHardy and Mr. J. F. Baker of Messrs. Cooper & Nephews S.Af. (Pty), Ltd., whose co-operation and assistance is gratefully acknowledged. Thanks are also due to Messrs. D. C. Goch and H. Marr for statistical analysis of results and to Mrs. X. Proimos, Mrs. M. M. Hall and Mr. M. J. van der Walt who assisted with the laboratory work.

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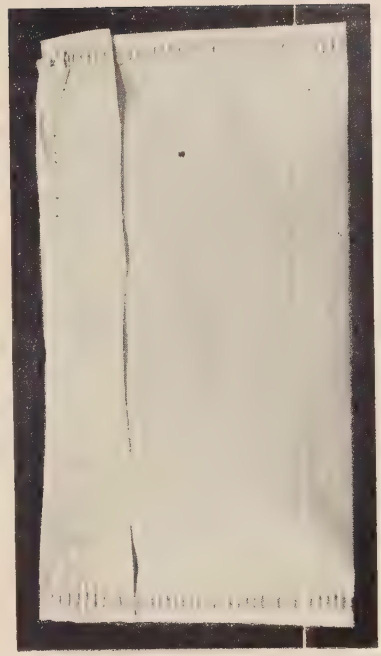


Fig. 2. Apparatus for separating tick larvae from insecticide suspension.

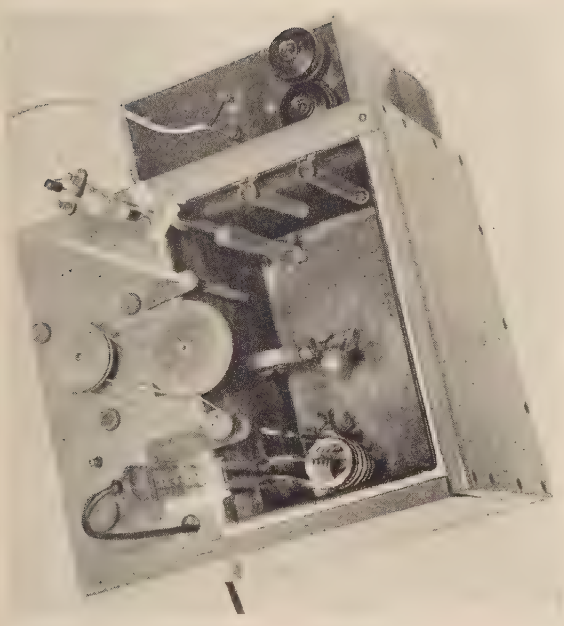
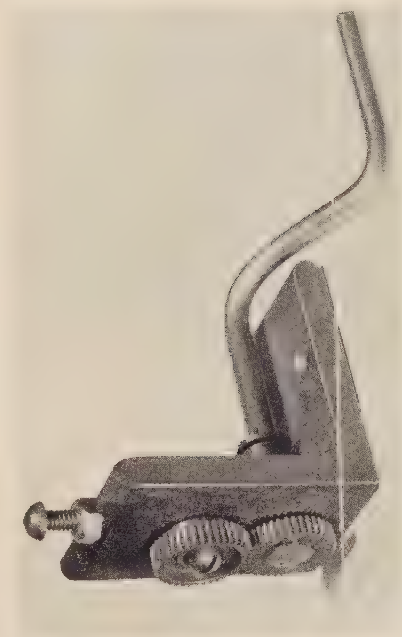


Fig. 1. Immersion apparatus.



REACTIONS OF INSECTS TO THE OLFACTORY STIMULI FROM THE COMPONENTS OF AN INSECTICIDAL SPRAY.

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and

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It has often been suggested, particularly in relation to mosquitos and other biting flies, that the freedom from adult insects after an aerial application of insecticide results more from the repulsion of insects out of the sprayed area than from their death within it. Some field observations support this suggestion (A. W. A. Brown, R. Hall, private communications). The preliminary laboratory studies here described were designed to throw some light on this matter.

Materials and Methods.

The materials tested in this work were the ingredients of the spray most commonly used in aerial applications of insecticide for mosquito control in Canada. These are technical DDT, diesel fuel oil, and a proprietary auxiliary

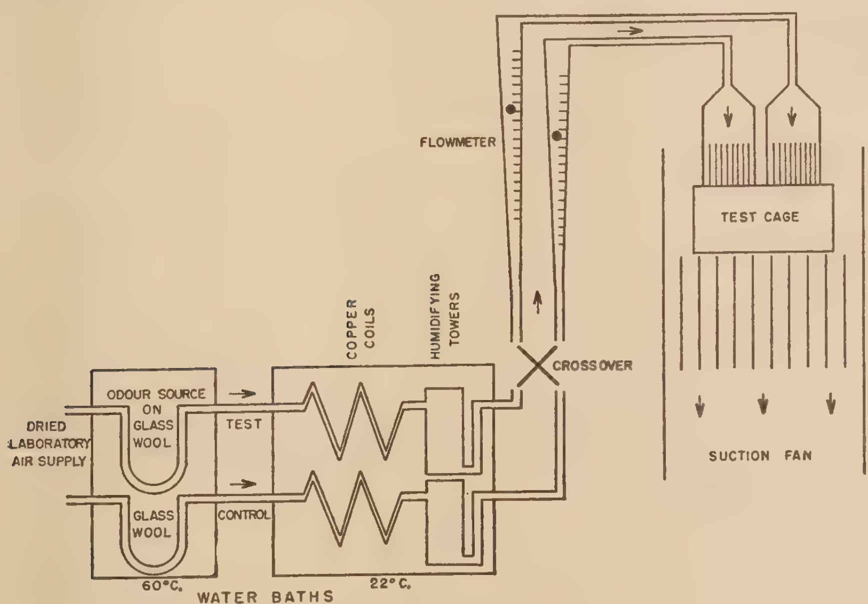

Fig. 1.—Diagrammatic representation of the vertical wind-tunnel olfactometer used in the tests at Suffield.

solvent, Velsicol AR50, which consists largely of methylated naphthalenes. The diesel fuel oil used in these tests was an Imperial Oil product from Pembina crude.

Studies were conducted independently at the Suffield Experiment Station (by I.S.L.) and at Edmonton (by B.H.), using completely different equipment. The equipment used in the Suffield experiments is shown in fig. 1. This was developed from the olfactometer described by Wieting & Hoskins (1939) but differed from it in that the test areas were horizontal and the air currents were vertically downwards.

The main vertical wind-tunnel consisted of a 12-in.-diameter glass cylinder 30 in. long with an exhaust fan at the lower end. Laboratory air supply was used for the test and control air streams which entered the top of the main tunnel through inverted Büchner funnels having $4\frac{3}{4}$ in. inside diameter. Turbulence was reduced in the main tunnel by a stack of brass tubes, $10\frac{1}{2}$ in. long and $1\frac{1}{4}$ in. in diameter, below the test cage and in the test air streams by stacks of drinking straws in glass extensions to the Büchner funnels. These extensions stood on top of the rectangular test cage which was 10 in. × 6 in. × $4\frac{1}{2}$ in. deep with glass sides, sheet metal ends, and 16-mesh wire screening at the top and bottom.

The test and control air streams from a laboratory compressed-air supply were dried over calcium chloride and passed through U-tubes containing glass wool in a water bath held at 60°C. The liquid test materials were dispersed on the glass wool in the U-tube in the test air stream; DDT was used in lump form, in between two plugs of glass wool. The air streams were then cooled to 22°C. in coils of copper tubing in a second water bath and in this bath were passed through towers of wet glass beads which raised the humidity of each stream to between 29 and 35 per cent. R.H. When liquids were being tested, condensation occurred in the test stream tower, indicating that the air was saturated or super-saturated with some component part of the material under test.

The pattern of air flow in the cage was checked by placing a piece of coarse white cotton gauze sprayed with phenolphthalein solution on the floor of it and then introducing strong ammonia into the test stream. The speeds of the suction fan and the test and control air streams were adjusted until laminar flow was indicated by the distribution of the red reaction colour in such a test. The final mean speed used in the test and control air streams, measured by tapered-tube flow meters, was 1·03 cm./sec. (7 litres/min.). That in the main tunnel was 31·7 cm./sec. Connections were arranged so that a rapid interchange could be made between the test and control air streams and the two outlet ports in the test cage.

Adult females of *Culex tarsalis* Coq., reared in the laboratory by the method described by Brennan & Harwood (1953), were used for the tests. These were taken at random in batches of about 50 from rearing cages containing several hundred. They were left in the test cage in darkness for 15 minutes before a flashlight was used briefly to make counts of the numbers resting on the test and control areas. Ten counts were made at three-minute intervals over a period of 30 minutes. Clean air was then passed through both ports for 15 minutes, the air streams were interchanged, and a further series of ten counts was made. Before tests with spray components were started, a test was run with the ammonia used to check the pattern of air flow since this substance was known to have repellent properties.

The method used at Edmonton was based on the assumption that an attractive odour induces an anemopositive reaction in an insect, that is to say, that insects will fly upwind when exposed to an air current which carries an attractive odour. This appears to be the most probable explanation of many field observations on the reactions of insects to odours (Kennedy, 1940; Schwinck, 1954; Danzer, 1956). The interaction between wind and odour is also mentioned by Warnke (1931),

Flügge (1934), and Dethier (1947). More recent work supporting this theory is discussed by Dethier (1957).

Many changes were made in the apparatus used initially before it reached the form used to obtain the results reported here (see fig. 2). Further improvements are now being made as a result of this work and will be reported in a later paper. The apparatus consisted essentially of a T-tube, across the top of which was passed a current of air to which odours could be added, and into the stem of which insects could be introduced. The repulsiveness or attractiveness of an odour was then measured in terms of the proportion of the insects which moved downwind or upwind.

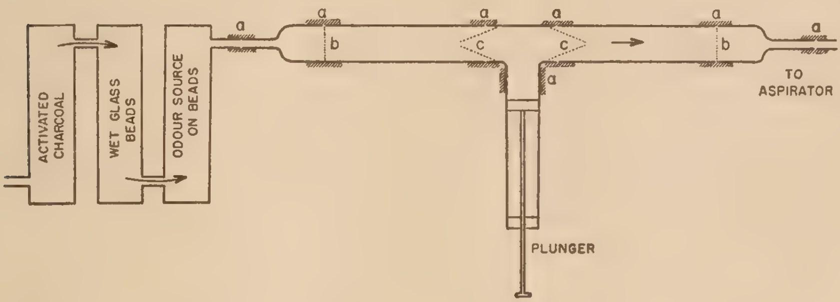

Fig. 2.—Diagrammatic representation of the T-tube apparatus used to evaluate olfactory reactions in tests at Edmonton: aa, transparent plastic tube couplings; bb, flat 20-mesh saran screen discs; cc, 45° 20-mesh saran screen cones.

The rates of air flow required, at least for the smaller insects, are small enough to permit the use of an aspirator bottle to draw the air through. In this simplest form the apparatus can readily be taken into the field and used with field-caught insects; some of the data on *Aëdes* spp. native to Alberta were obtained in this way. If a compressed-air supply is available in the laboratory, this is more convenient.

Pyrex glass T-tubes, of inside diameter from 15 to 39 mm., were used for all of the data reported here. The T-tubes themselves were made with stems and arms just long enough to hold coupling sleeves of transparent polyvinyl chloride ("tygon") tubing of a grade claimed by the manufacturers to be odourless. Lengths (20 cm.) of pyrex tubing of the same diameter were coupled to the stem and to each side arm. The ends of all tubes were ground flat and butted against each other to minimize contact of the air stream with materials possibly capable of contributing or adsorbing odour. A 45° cone of 20-mesh saran screening was press-fitted into each arm of the T; the apices faced outwards and were truncated sufficiently to permit the passage of the insects under test. This prevented insects from returning into the T. The plastic couplings allowed the side arms to be removed for counting specimens and to be reattached to the stem of the T if the insects were to be passed through the apparatus again. With some insect species and some odours it was found possible to run the same batch through the tube several times in succession before adaptation was manifest; usually, a batch was not used more than twice on any one day, and was kept in a well ventilated place between runs. Insects reluctant to pass into the top of the T were helped in with a plunger tipped with sponge rubber.

Before any tests with odours were conducted with a species, a series of runs was made using air which had been through a 250-ml. tower of activated charcoal to remove laboratory odours and a similar tower containing wet 3-mm. glass beads

which brought the humidity to between 70 and 80 per cent. R.H. Under these conditions the speed of flow was adjusted until about 50 per cent. (between 40 and 60%) of the test insects moved upwind and 50 per cent. downwind; a typical relationship between speed of air stream and percentage of insects moving upwind is shown in fig. 3. The incident light from either side along the axis of the arms of the T as measured by a photographic light meter was roughly balanced before each test, in the laboratory by manipulating window blinds and in the field by rotating the table on which the tube was mounted. Two runs were then made in quick succession with the same insects, one with the air flow in one direction and the second with the flow reversed. In successive tests (pairs of runs) the direction of flow for the first run was alternated. Except for some of the earlier tests, about 100 insects were used in each batch. The percentages moving upwind for the two runs of a test were averaged. Before each series of tests with a particular odour, a test with moist air alone was run. This served as a check that the batch of insects was behaving normally in this respect, that there was no residual odour from previous tests with other materials, and also to accumulate adequate data on the normal percentage moving upwind under these conditions. The importance of this last point will be clear from the method of calculating the results. Usually, two sets of tubes were available in each size; these were used on alternate days, were washed after use, and were aired while they were not in use.

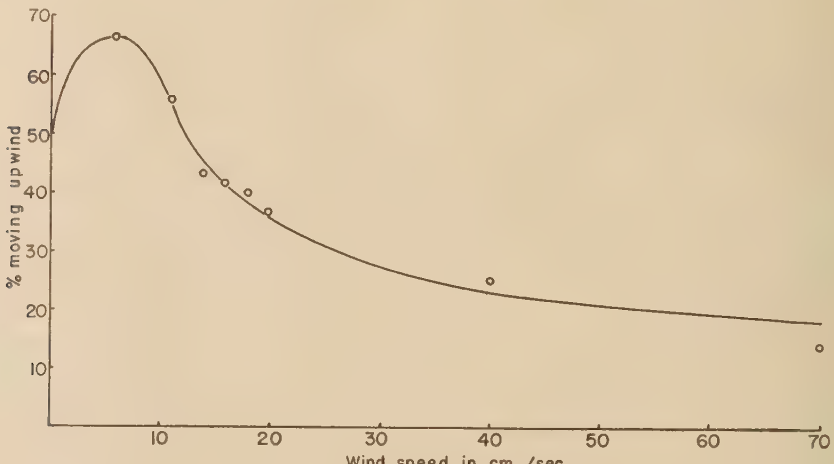

Fig. 3.—The relationship between wind speed and percentage of adults of *Drosophila* moving upwind in moist air.

Liquid test materials were dispersed on 3-mm. glass beads in 250-ml. towers which were inserted in the flow train after the water tower. DDT was first tested by placing lump technical DDT in such a tower; particulate material was screened out with packed cotton. A pronounced repellent effect was at first manifest with DDT. For a few minutes at the start of a test nearly all the species of Diptera tested went downwind but with the continued passage of air there were soon equal numbers turning in each direction. The tower was therefore replaced by a two-gallon bottle loosely filled with lumps of technical DDT. This apparently contained enough air, charged with DDT vapour, in the interspaces for a complete test. It was allowed to stand overnight for further volatilisation to take place between tests; this procedure gave consistent results.

The insects tested by this method were: *Drosophila melanogaster* Mg., reared in the laboratory on a standard maize-meal medium; *Aëdes aegypti* (L.), reared in the laboratory by the method described by Trembley (1955); *Musca domestica* L., two strains reared in the laboratory by the method described by Fisher & Morrison (1950), one from Suffield Experimental Station, and one from Namao, Alberta, which showed a 20 × resistance to DDT; a Chloropid fly, *Thaumatomyia glabra* (Mg.), trapped from wild populations; *Aëdes* spp., wild-caught blood-hungry females consisting principally of the following species: *A. vexans* (Mg.), *A. stimulans* (Wlk.), *A. excrucians* (Wlk.), *A. fitchii* (Felt & Young), *A. canadensis* (Theo.), and *A. intrudens* Dyar. Approximately equal numbers of each sex were used for all insects except the wild-caught species of *Aëdes*. The numbers of *Drosophila* and of *M. domestica* were counted separately by sexes after several tests but no consistent behaviour differences between sexes were found.

The materials tested are complex mixtures; this made it impossible to measure precisely the concentrations of the vapours used. Since we believe that, during an aerial application of insecticide, conditions approaching saturation, at least of the more volatile components, are to be found for a significant time in the area being sprayed, an attempt was made to obtain concentrations as high as possible. Estimates of the actual concentrations produced were obtained by dispersing 2·5 g. of material over a known surface area of glass beads and then passing air over these at a known rate and recording loss in weight with time. The weights of materials taken up by the air during a normal test with a 28-mm. bore T-tube and air speed 12 cm./sec. (4·43 litres/min.) calculated by extrapolation from these data, are shown in fig. 4; the gradually decreasing slope is attributed to the

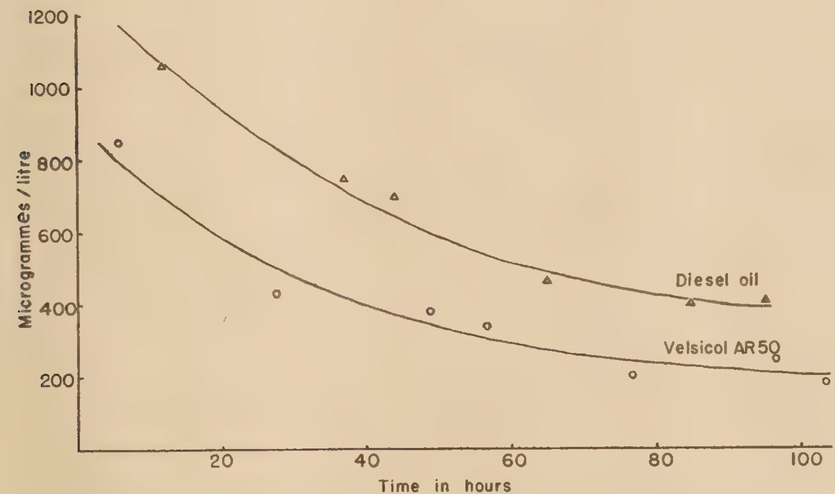

Fig. 4.—The relationship between the concentration of materials from the odour sources in the air and the time in hours. 28-mm. bore T-tube, air speed 12 cm./sec. (4·43 litres/min.).

selective evaporation of the more volatile components in the early stages. This is in accord with the observation that if many tests were run without changing the material in the tower, the response gradually decreased. We do not know, however, the relative proportions of the different components in the original liquids nor in the vapours to which the insects were exposed.

A series of tests was conducted with *Drosophila*, using aqueous solutions of acetic acid as the odour source to confirm that attractiveness was manifested by an upwind reaction. This confirmation was obtained at concentrations below one per cent. and maximum attractiveness was shown at about 0·5 per cent.

Results.

In the tests at Suffield, the proportion of the mosquitos in the test cage which settled on the test areas usually lay between one-third and two-thirds of the total number in the cage. This means that each count was based on about 25 reacting individuals, which were, however, the same individuals for the most part, for each count in a series.

In the Edmonton tests, there was some wastage of insects between the tests, and one individual was rarely used for more than three or four tests. While some examples crawled on the surface of the tube and proceeded either upwind or downwind, most of them, especially fresh individuals, flew and reacted on the wing. Crawling was a more common habit on the downwind than on the upwind side. With materials that gave a downwind reaction a reluctance to enter the current at the top of the T was observable, and a very high proportion of the individuals which had to be helped into the current with the plunger, reacted downwind.

TABLE I.

Olfactory responses of adults of some Diptera to the vapour of spray components and other materials.

Species	Fuel oil	Velsicol AR50	DDT	Complete spray	Other materials
Drosophila melanogaster	$-0{\cdot}54 \pm 0{\cdot}030$ (14)	$-0{\cdot}80 \pm 0{\cdot}022$ (15)	$-0{\cdot}42 \pm 0{\cdot}048$ (16)	$-0{\cdot}72 \pm 0{\cdot}031$ (14)	0·5% acetic acid $+0{\cdot}24 \pm 0{\cdot}054$ (13)
Musca domestica (Namao strain)	$-0{\cdot}28 \pm 0{\cdot}042$ (10)	$-0{\cdot}40 \pm 0{\cdot}035$ (8)	—	—	—
Musca domestica (Suffield strain)	$-0{\cdot}36 \pm 0{\cdot}065$ (11)	$-0{\cdot}58 \pm 0{\cdot}049$ (9)	—	—	—
*Thaumatomyia glabra**	—	$-0{\cdot}42 \pm 0{\cdot}033$ (4)	—	—	—
Aëdes aegypti	$-0{\cdot}16 \pm 0{\cdot}054$ (6)	$-0{\cdot}34 \pm 0{\cdot}050$ (8)	—	—	—
Wild-caught *Aëdes* spp.	$-0{\cdot}42 \pm 0{\cdot}030$ (11)	$-0{\cdot}58 \pm 0{\cdot}038$ (8)	—	—	
Culex tarsalis	$-0{\cdot}16 \pm 0{\cdot}030$ (10)	$-0{\cdot}81 \pm 0{\cdot}040$ (19)	$-0{\cdot}42 \pm 0{\cdot}029$ (10)	$-0{\cdot}32 \pm 0{\cdot}047$ (22)	Strong ammonia $-0{\cdot}88 \pm 0{\cdot}017$ (29)

Each entry represents the mean ± standard error of the mean, followed (in brackets) by the number of readings.

(0 = neutral, +1·0 = maximum attractiveness, −1·0 = maximum repellency.)

* No check against moist air for this species.

Initially, the raw data were recorded and means and standard errors were calculated. Results by the methods used at Suffield and at Edmonton with related insects were clearly not directly comparable; nor, expressed in this form, were they of any more general use. They were therefore transformed to give what we term an olfactory response figure for each species, odour, and concentration, such that the maximum repulsiveness would be represented by $-1{\cdot}0$, the maximum attractiveness by $+1{\cdot}0$, and neutrality by 0. This was done for the Suffield data by subtracting the number of insects resting on the check area from the number resting on the test area and dividing the result by the total number resting. For the Edmonton data the percentage moving downwind was subtracted from the percentage moving upwind and the result divided by 100. Percentages were corrected for any deviation from 50 per cent. of the cumulative percentage moving upwind in moist air (obtained from the initial check tests of each series) by multiplying by 50 and dividing by this cumulative percentage. Thus, if the cumulative percentage moving upwind in moist air were 53·4 and the percentage in a given test with moist air *plus* an odour were 43·2, the corrected percentage moving upwind in the odour would be $\frac{43{\cdot}2 \times 50}{53{\cdot}4} = 40{\cdot}4$ and the olfactory response figure would be $\frac{40{\cdot}4 - 59{\cdot}6}{100} = -0{\cdot}192$. Means and standard errors of the means were then recalculated. The results obtained by both methods are summarised in Table I.

Discussion.

Clearly, there are components in diesel fuel oil, in the auxiliary solvent tested, and in technical DDT which are markedly repellent to several insects, including species against which these materials are regularly used. The olfactory response to the completed spray is intermediate between the responses to the ingredients. In the field, this repellent property may be expected to result in a reluctance of insects to settle in a sprayed area (vertical wind-tunnel) and in a tendency to move downwind (T-tube).

Although repellent effects of DDT have long been known (Gahan & others, 1945; Kennedy, 1947) the effect reported here differs in that contact with the solid substance was precluded in both methods of test. Equally, in both methods, however, the effect may be due to a relatively volatile impurity, probably without insecticidal activity.

The three series of tests with mosquitos, in which both kinds of equipment were used, all indicated that Velsicol AR50 was considerably more repellent than fuel oil.

Whatever the true nature of the materials which caused the reactions observed, the practical implications are clear: that many spray ingredients contain materials which tend to defeat the object of the spray by inducing such reactions in insects exposed to their vapour that the insect will not come into contact with the toxicant.

This provides an additional argument for the procedure, usually recommended in aerial and sometimes in other methods of spraying, of moving upwind on each successive pass (Anon., 1954), since by this procedure insects repelled out of the later swathes have to pass through the already sprayed area. With the reverse procedure the odours of the first swathe, carried downwind through the target area, would provide warning in time to permit insects to move out through unsprayed territory. Selective survival of individuals showing these reactions may be a factor in the development of behavioural resistance to insecticides. Our resistant strain of house-flies, however, showed a somewhat lower sensitivity than did the supposedly normal strain. It is suggested that the elucidation of the true

nature of the materials responsible for these reactions, with a view to eliminating them and perhaps replacing them by attractive ingredients, would be worth-while.

Summary.

Two kinds of equipment for measuring the reactions of insects to the olfactory stimuli provided by some common components of insecticidal sprays are described. One of these, consisting of a T-tube carrying a current of odorous air across the top and admitting insects up the stem, is new, can be used in the field, and gives rapid and reproducible evaluations. Tests with several species of Diptera showed that technical DDT, diesel fuel oil, and an auxiliary solvent containing methylated naphthalenes are all strongly repellent or contain strongly repellent components. Related species gave similar results with the two kinds of equipment. House-flies (*Musca domestica* L.) resistant to DDT were less sensitive than normal house-flies. The implications of these findings are discussed.

Acknowledgements.

B. J. Wenner and R. D. McMullen helped with the development of the method used at Suffield and K. R. Depner and J. M. Hepburn with that used at Edmonton. Most of the tests at Edmonton were conducted by E. M. Collett and J. C. Shore. Cultures of insects were kindly provided by J. M. Brennan of the U.S. Public Health Laboratory at Hamilton, Montana, and by R. W. Fisher of the Science Service Laboratory at London, Ontario. Funds were provided for the work at Edmonton by the Canada Department of Defence Production.

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BIOLOGY AND ECOLOGY OF THE GARDEN CHAFER, *PHYLLOPERTHA HORTICOLA* (L.).

IV.—THE FLIGHT SEASON: INTRODUCTION, AND GENERAL ASPECTS.

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The flight season of the Garden Chafer, *Phyllopertha horticola* (L.), is the period of adult activity above ground. As will emerge later in this series, ecologically it is a very important period in the life-cycle. Apparently only four papers on the Garden Chafer include some description of the flight season: (a) Rittershaus (1927), (b) Thomas & Heal (1944), (c) Gray, Peet & Rogerson (1947) and (d) Raw (1951). Rittershaus worked near Berlin, the others in England. Excepting a few sex ratios confined to the first 11 days of the flight season (c, d), none of the papers gives any quantitative data, nor a clear indication of the pattern of events in time-table form. The following is a composite summary of the four accounts (with, in square brackets, some questions and comments by the present writer):—

The flight season starts in May or June (a, b, c, d) according to the weather (c, d) and lasts 3–4 weeks (a, b, c, d). The first adults seen above ground are males (d). With (a, b, c) or without (c, d) a prelude of small numbers active for a few days, most of the population [what proportion?] emerges abruptly (a, c, d) and swarms at first over the grass sward (a, b, c, d). Later in the season [when?] the beetles congregate on surrounding bracken, bushes and trees (a, b, c, d). They fly only when the sun shines, starting between 9 and 10 a.m. (a, c, d). On the first day they all go back into the sward after activity (c) [does this behaviour continue?]. From about one hour on the first day, the daily activity progressively lengthens (c, d); but "it is only when the flight period is well advanced that the beetles are active to any extent after 2 p.m." (d); the main activity, however, is in the forenoon or "from 11 a.m. to 1 p.m." (c) [is the latter British Summer Time, or sun time which would be 10 a.m. to 12 noon Greenwich Mean Time?]. Males appear earlier in the forenoon than females (a). The males, flying and perambulating, search for the females, the latter spending most of the time eating (a). More males than females are seen throughout the season (a, c, d) except at the very end (c, d). Apart from that, the male/female ratio increases (c), decreases (d) as the season progresses [contradiction!]. Feeding—on grasses, herbs, bracken, bushes, trees (a, b, c, d)—and mating go on throughout the season (a, b, d). Mating takes place in the forenoon and the female may be clasped for several hours (a, c, d) though the actual coition is shorter (a) [how short?]. Immediately after coition some females try to get down into the soil despite the clasping male but usually they first wander around for hours, carrying the male and feeding (a) [obviously this is an interesting divergence in female behaviour requiring investigation]. Males remain above ground (a), but (see before) not apparently in the early part of the season (c). "The adults live for 10–14 days" (c) [no proof given]. One author (d) holds

* Agricultural Research Council Unit of Insect Physiology.

that the beetles " do not spread far from their place of origin ", and interprets another (a) as stating the opposite. However, the latter author merely says that " the main host [of beetles] came out between 9 and 10 a.m. and towards noon they had dispersed over the whole area "; there is no indication that the said " area " was anything more than the field studied and its surrounding bushes and trees.

Plainly the published information on the flight season is incomplete and rather vague even where it contains no contradiction; in some respects it is also erroneous (see later). This first instalment of the present study of the flight season deals with the general or mass aspects of Garden Chafers engaged in it.

Location of the Study.

The flight seasons of 1948–1952 have been studied broadly on six fields in the English Lake District—four fields at Buttermere and one each at Keswick and Ambleside. The general picture of events has been the same in all of them. In two of the Buttermere fields observations were made daily. Here again there was the closest similarity down to the smallest detail, except that, due to a difference of altitude, everything happened a few days earlier in one field than in the other. A description of happenings in one of these two fields may therefore be taken as typical of flight seasons in the Lake District. The chosen field is Upper High House, Syke Farm, Buttermere, and unless otherwise noted the data of the present paper refer always to this field.

Upper High House Field, U.H.H.F., is an old " intake " pasture which had not been ploughed for at least 70 years.* It is approximately a rectangle 200 yd. × 100 yd. (4 acres) near the foot of the fell running alongside Crummock Water. Its length lies horizontally across the slope of the fell. It is bounded more or less entirely by several small woods (mainly oak trees) and old attenuated overgrown hedgerows (mainly hawthorn).† Bracken extends in from the edges to a depth of 10–20 yards all round, leaving free an inner 3-acre rectangle of pasture dominated by *Agrostis tenuis* and *Festuca ovina*. In effect then, the field presents a roughly rectangular area of open grass sward surrounded by a belt of bracken bounded by trees and hedge. The field has a southern aspect. The soil is light and shallow (3·6 ± 0·1 in. deep); the land slopes (on the average about 1 in 7). and hence drainage is good. In many respects U.H.H.F. is typical of infested fields in the Lake District.

The beetle population in this field is largely self-contained (see later paper). Behaviour was uniform throughout the field and so, to economise in space and because observations covered a longer period in that half, the numerical data for the western half alone will be given.

Starting Date and Duration of the Flight Season.

The starting date for the flight season over the years 1948 to 1952 varied from 21st May in 1949 to 8th June in 1951 (Table I). The date when the first adults emerge above ground naturally depends on preceding soil temperatures. The latter are affected not only by atmospheric temperatures over the ground surface and by solar radiation, but also by rainfall, since wetter soil takes longer to warm up and, in May–June, soil is usually cooled by rain.

Starting dates in neighbouring fields may differ in the same year because of differing soil temperature conditions. Thus in the adjacent field, 100 ft. lower down the fell than U.H.H.F., the flight season has started 6, 2, 2, 4 and 2 days earlier, respectively, in the successive seasons 1948–1952. All events subsequent

* Eastern half ploughed up in 1950, western half in 1953 after this study was completed.
† The hedgerows were cut down between 15th January and 19th February, 1951.

to the start (see later) are naturally also earlier in this lower field. Drainage is similar in the two fields but the lower one is much more sheltered (topography and trees) and hence warms up sooner. On the other hand the flight season always starts several days later in another field which is also adjacent to U.H.H.F. This particular field is at the same level, with the same degree of exposure, but has a deeper, wetter soil. By reason of poorer drainage, therefore, it takes longer to warm up and the flight season is accordingly retarded.

TABLE I.

Flight seasons, 1948–1952.

Year		1948	1949	1950	1951	1952
Beetles seen	First	24.v.	21.v.	2.vi	8.vi.	22.v.
	Last	1.vii.	30.vi.	28.vi.	4.vii.	15.vi.
Duration of flight season (days)		39	41	27	27	25
Totals days with	No activity ..	13	7	7	6	4
	Some activity	26	34	20	21	21

The duration of the flight season may sometimes be considerably longer than previous authors observed. In 1948 and 1949, beetles could be seen flying for 39 and 41 days, respectively, after the first individuals appeared; in 1950, 1951 and 1952 for 27, 27 and 25 days, respectively (Table I). Thus the flight season may on occasion extend over 5–6 weeks.

From previous work (see p. 685) a season length of 3–4 weeks, as in 1950–1952, is to be expected. But a jump to 5–6 weeks, as in 1948 and 1949, is intriguing. For convenience, seasons 1950, 1951 and 1952 will be called " shorter seasons " and 1948 and 1949 called " longer seasons ".

A possible reason for the occurrence of longer seasons is a greater incidence of weather which hinders or prevents activity after the season has begun. However, comparisons of (a) numbers of inactive days, (b) total hours of daily activity, (c) hours of bright sun in (b), and (d) mean shade temperatures in (b) over the first *three* weeks revealed no significant differences between longer and shorter seasons.

Another possible reason is a longer period of emergence for the population. Obviously, if some parts of a field warmed up much earlier than other parts, then population emergence, and therefore the flight season itself, would be that much prolonged. Now in searching for food in autumn, birds turn over the turf severed by third-instar grubs. They are able to do this only where and when the grub population is so dense that severance of the roots is practically complete (and density of the grubs varies in space as well as time). On turning over turf, birds do not find all the grubs because some have already penetrated more deeply in order to hibernate (see Milne, 1956). The loose turf is mostly blown away downhill by the winds. Some of the ground so bared is still not re-clothed with herbage by the following flight season, and where it is re-clothed the cover is shallower and more open than is the case with the surrounding undamaged sward. In late spring the soil of a bare or poorly covered patch (if not too small) naturally warms up more quickly in the sun, thus hastening development of Garden Chafers there. Sampling has revealed a general developmental difference of at least a week (probably more) between Garden Chafers from the soil of large bare patches and their neighbours from under the adjacent more highly insulating undamaged sward. In the flight seasons of 1948 and 1949, there was much bare ground

(including many large patches), in 1950 very little (all small patches), in 1951 practically none and in 1952 none at all (quantitative data will be given in a later paper on sward damage). Clearly the " longer seasons " of 1948 and 1949 can be attributed mainly to the lengthening of the emergence period which was due to the state of the sward in those years.

The only other circumstance possibly contributing to the making of longer seasons is population size. It is well known that range of any biological characteristic, such as individual length of life, tends to extend with the number of individuals. The U.H.H.F. population was enormously greater in 1948–49 than in 1950–52 (as evidenced by sward damage—see above, and see also actual Garden Chafer densities to be given in a later paper). Hence in 1948–49 there may have been some longer-lived individuals present which helped to make the flight season longer in those two years.

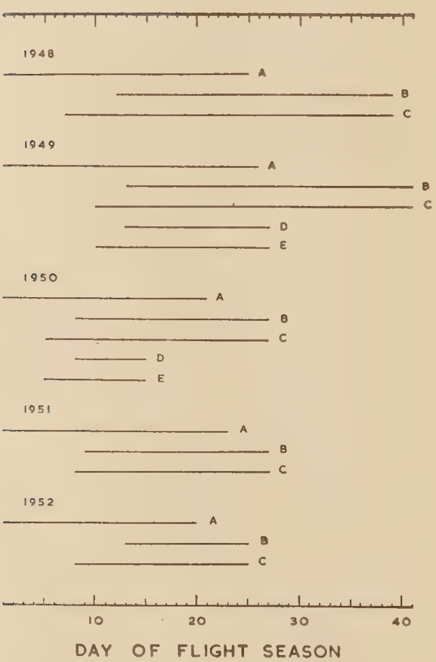

Fig. 1.—Duration of phases of activity of *P. horticola*, and other details: A, swarming on grass sward (Phase 1); B, swarming on bracken (Phase 2); C, resting all night on bracken; D, swarming on hawthorn (in Phase 2); E, resting all night on hawthorn.

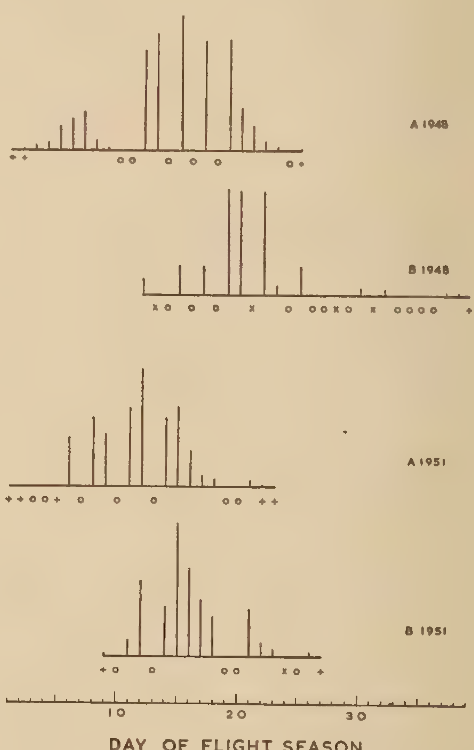

Fig. 2.—Day to day relative numbers of beetles (*P. horticola*) in each phase of activity. Duration of phase shown by horizontal line; vertical lines indicate relative numbers from day to day (*i.e.*, average densities per unit area). A, Phase 1 (swarming on grass sward); B, Phase 2 (swarming on bracken); + = some beetles active but not sufficiently numerous to show on the histogram; × = beetles active but density not measured; O = no beetles active because of weather.

The Two Phases of Activity.

As will be seen later, the number of beetles rises to a peak, then falls, during the active period of each day. Peak densities of active beetles were recorded daily in the flight seasons of 1948–1952. This was done by counting all the individuals seen on fixed square yards marked by pegs driven into the ground. These fixed square yards were distributed evenly over the open grass sward and bracken fringe. The same square yards of grass sward were observed every year with some additions: there were 16 square yards in 1948; 22 further square yards were added in 1949, making a total of 38; 6 more were added in 1950, making 44; and these 44 were all retained in 1951 and 1952. Within the bracken fringe the same 6 fixed square yards were used every year except 1949 when the population of 20 fixed bracken plants was counted instead. On each day of observation, all the square yards were counted quickly one after another as soon as numbers appeared to have reached their peak. The routine took from 10 to 20 minutes according to weather conditions and density of beetles. With growing experience, it was seldom that the daily peak was wrongly anticipated so that counts had to be repeated. On the grass sward, the total beetles per square yard could be counted fairly easily even in hot sunshine. On the bracken this was rather less easy, and, whenever the opportunity allowed, counts were speedily made as a cloud passing over the sun caused all beetles to alight temporarily on the fronds. Counts on ten branches of hawthorn (1949, 1950) were made by the same expedient as for bracken except that the temporarily-settled beetles were made to fall down on a white sheet by shaking the branches.

Raw (1951) says: " A characteristic feature of emergence into activity is the abruptness with which it begins. For a few days occasional beetles may be seen, then quite suddenly there is a mass emergence. . . ." Among the five seasons observed, 1951 was the only one in which an approximation to Raw's description was noted. Since the curve of numbers of individuals emerging each day from the pupal skin rises fairly smoothly to a peak (then falls in the same way—see Milne, 1956), one would not expect the emergence into activity of the population to be abrupt. Nor is it so, unless weather conditions interfere. Thus in 1948, 1949, 1950 and 1952, because weather did not interfere unduly in the first week of the season, numbers started low and showed an unmistakable tendency to build up gradually to a peak, taking 15, 19, 10 and 9 days in the process for the respective years, *i.e.*, there was no abruptness in the emergence (see fig. 2, A 1948 as illustrative, and note that here the fall in numbers from the 8th to the 11th day was due to weather deteriorating). In 1951, on the other hand, very few or no beetles were seen on the first five days but on the 6th day an average density of 4 per sq. yd. appeared abruptly on the scene (see fig. 2, A 1951). The first day of this flight season was sunny and warm, but weather on the subsequent four days was so unfavourable that it gave extremely little opportunity (2 days) or no opportunity at all (2 days) for beetles to come to the sward surface and show themselves in activity. On every one of these four days, additional beetles would be ascending from their hibernation cells and accumulating at the bottom of the sward, ready to emerge into activity (see Milne, 1956); hence the apparently abrupt mass emergence on the sixth day when the weather became favourable again. This is the sort of phenomenon Raw must have witnessed but it is certainly not characteristic.

A and B in figs. 1 and 2 * show that there were invariably two distinct though overlapping phases in a flight season at Buttermere. In Phase 1 (20–26 days, depending on the total length of the season), the beetles, during activity, swarm over the grass sward from which they have emerged. In Phase 2 (13–29 days)

* In figs. 1–3, a day is denoted by the perpendicular itself and *not* by the space between two perpendiculars on the scale.

they swarm on the bracken bordering the grassy arena and on the hawthorn hedge (D, fig. 1) bounding the bracken fringe; a very small proportion goes to other trees such as oak and hazel. Over the years, Phase 2 started 8–13 days after the beginning of Phase 1; the overlap when the population was transferring its attention from grassy arena to bracken fringe occupied 8–15 days, leaving 5–16 days of Phase 2 alone at the end. Thus the beetles begin by working over the grass sward, and gradually switch over to working in the bracken fringe. Obviously overlap of the phases is the result of population emergence extending in time: earlier beetles enter phase-2 activity before later beetles complete Phase 1.

A curious feature of Phase 2 is that although beetles begin to work on both bracken and hawthorn on the same day, they nevertheless abandon the hawthorn (and other trees) in the latter half of the phase, confining themselves then wholly to the bracken (see B & D, figs. 1 & 3). The reason for this is an unsolved

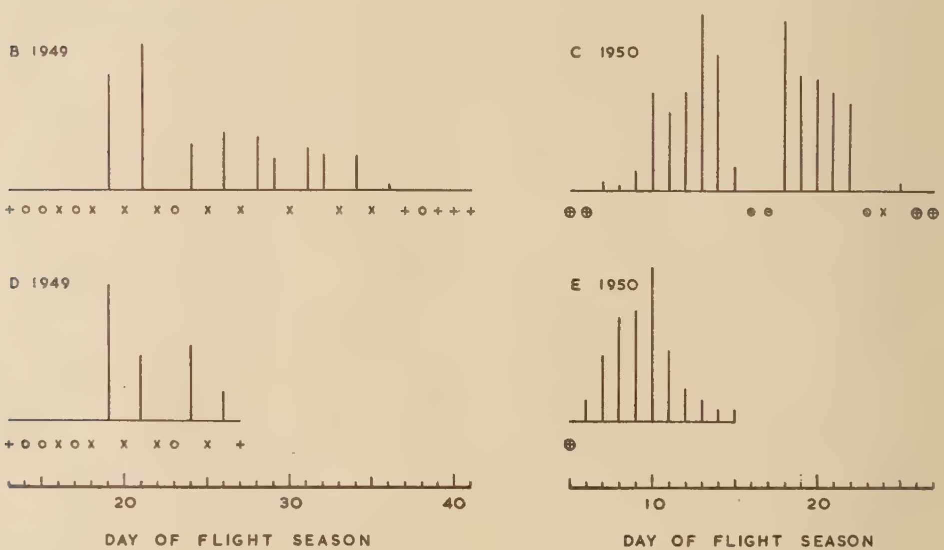

Fig. 3.—Day to day relative numbers of beetles swarming on bracken (B) and on hawthorn (D) in 1949, and resting all night on bracken (C) and on hawthorn (E) in 1950. ⊕ = some beetles present but not sufficiently numerous to record on histogram; ⊙ = no beetles present because of weather during preceding 24 hours (see text in connection with Table III); other symbols as in fig. 2.

problem. In both years of observation (1949 & 1950), the period on hawthorn ended with the disappearance of the blossom. The beetles certainly ate some of the flower petals but they also fed largely on the fruits and leaves, and the latter were, of course, still available long after all the flowers had disappeared. Could the explanation have been scent attraction ?

The main purpose of activity must be to facilitate the meeting of the sexes. Over the grass sward, *i.e.*, in Phase 1, the beetles alternate between flying (weaving at an average height of about 9 in.) and running or walking and resting. One characteristic of this activity is randomness so that individual progress in one direction is more or less cancelled by that in another. Within the bracken fringe, *i.e.*, in Phase 2, precisely the same kind of activity takes place, only now

it occurs on the upper fronds of the bracken plants instead of on a relatively plane surface as on the grass sward of the arena.

After Phase 1 is finished, *small* numbers of beetles are still seen over and on the grass sward right up to the end of the season. Their behaviour now, however, has quite a different character from that in Phase 1. No longer do they swarm low over the grass or run aimlessly over its surface. Now they are either flying high on a straight course right out of their own field, or, if they land in their own field, digging into the turf almost as soon as they alight. These, for want of a better term, have been called the " bee-liners ", a small proportion of Phase-2 individuals which break away from the mêlée of activity on the bracken fringe and trees. More will be said of the bee-liners in later papers.

Activity and the Weather.

Activity (*i.e.*, flying, running or walking over the vegetation) is governed by weather. The beetles are most active in bright conditions and indeed will fly and run only when the sun is shining. Among others, Raw (1951) has remarked how beetles drop to the ground when a passing cloud covers the sun and rise to fly soon after the sun peeps forth again. If the obscuring of the sun is short the beetles may walk about or wait immobile on the sward surface, but if it is so long and intense that the temperature falls they may disappear down into the mat for the time being. On warm bright-overcast days they may walk about quite busily on the grass, particularly after one or two days entirely unfavourable to activity, for then they seem very eager to be active, an eagerness that might be attributed to pent-up mating urge. On cold dull-overcast days, with or without wind or rain, they do not stir at all. All this has been said in reference to phase-1 activity, but it applies equally to Phase 2 except that the beetles never disappear in bad conditions (at least not the same day—see later) but remain in view, settled immobile on the upper fronds of the bracken.

From the foregoing description one might conclude that both warmth and light intensity are concerned in the degree of activity. In nature, it is quite easy to see the effect of temperature. For instance, on a sunny day with a cool strongish east wind, beetles fly only where sheltered to some extent from the wind by the lie of the land or by hedges and trees. This is clearly the influence of warmth since beetles will fly outside shelter in a stronger but warmer wind: in such case, if in Phase 1, they swarm closer to the ground than the usual average of about 9 in. and drop at each gust so that they are not carried away. The effect of temperature is obvious also in the fact that beetles practically never become active before 8 a.m.* (and usually one or two hours later), even when the sun has already been shining for hours from a clear sky.

It is less easy in nature to distinguish light effect as such. The fact that the beetle flies only in sunshine may be mainly a heat effect, *i.e.*, the dark body being warmed to flying pitch by radiation (provided its surroundings are not too cold as is the case before 8 a.m.). This is suggested by the short lag (30 seconds or more) between the reappearance of the sun and the re-start of flying after a cloud has passed over, even on a warm day. If the light component of sunshine alone controlled flying the lag would be less appreciable. Nevertheless, light intensity must have some effect because walking will start when dull-overcast turns to bright-overcast without any appreciable change in air temperature, and in this case there can be very little change in heat radiation taking place. The related effects of light and temperature, however, could only be determined by laboratory experiments.

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*N.B. In this series, time of day is always Greenwich Mean Time. It should be noted that the flight season occurs during the period of British Summer Time, and B.S.T. (clock time) is one hour in advance of G.M.T. (sun time).

Daily Duration of Activity in the Population.

The timing and duration of the activity period were noted daily throughout each of the five flight seasons, 1948–1952. The results for 1949 and 1952 are illustrated in fig. 4.

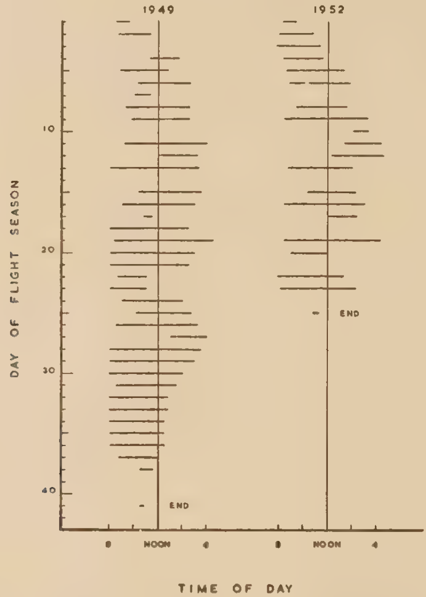

Fig. 4.—Daily duration of activity. Duration each day shown by a horizontal line. Time = Greenwich Mean Time.

Activity never started much earlier than 8 a.m. except on the 6th (7.15 a.m.) and 7th (7.00 a.m.) of June 1950, two days (at the end of an unusually hot sunny period) when shade temperature was already over 21°C. at 7 a.m. Omitting these two days, activity commenced at any time between 8 a.m. and 2 p.m., according as weather permitted, and the starting temperatures (shade) ranged from 5·6–17·7°C. The latter range is very wide but shade temperature is, of course, a poor indicator of conditions affecting beetle activity. In direct sunshine the beetle's body warms up faster than the air, so that activity starts at a relatively low shade temperature. In bright-overcast conditions the beetle is warmed mainly by the surrounding air and activity will therefore not start until a relatively high shade temperature is reached.

The first day of the flight season is usually marked by a rather short period of activity, 1–2 hours, in the forenoon (the exception being 1950 with 3 hr. 40 min.) no matter whether weather conditions continue favourable into late afternoon. As the days pass, the period lengthens until, given the requisite weather conditions, the beetles are active up to about 4 p.m., the latest time recorded being 4.30 p.m.

Previous authors give the impression that the lengthening of the activity is a regular process, but this is rarely so because weather conditions are rarely the same for several days at a time. The lengthening process tended to be regular in the early part of the flight season in 1952 (see fig. 4) and 1948, because the weather

remained fairly steady; but in the other three years there was little sign of a regular lengthening in the early days (*e.g.*, fig. 4, 1949), the extreme of irregularity being manifested in 1951 when the activity periods of the first nine days were 1½ hr., 1½ hr., nil, nil, 40 min., 30 min., 7 min., 5¼ hr. and 6½ hr., respectively.

On the other hand, previous authors had not noted that the daily activity period shortens towards the end of the season. This process is again rather irregular in most seasons but in 1949 was almost entirely regular. In the latter year an anticyclone prevailed from the 28th to the 37th day of the flight season. During these ten days the sun shone daily in a cloudless sky from sunrise to sunset. The steady decrease in the activity period from 7½ to 3¼ hours over that interval is shown in fig. 4. This must have been due to the senescence of the population, for activity became steadily more sluggish each day. But it is difficult to suggest a plausible explanation for the reverse occurrence at the beginning of the flight season.

The longest periods of activity, approximately 8 a.m. to 4 p.m., were naturally recorded when the sun shone all day after the first week of the season had passed. It will be noted that activity at this time, unless obviously affected by weather conditions, began and ended at the same distance from noon. This again suggests the influence of light intensity (see before), since light value will be the same at the beginning and end. However, activity occurs in bright-overcast conditions and the latter have a lower light intensity than sunlight four hours distant from noon. Hence the ending of activity at 4 p.m. on a cloudless day may well be due merely to fatigue of the beetles.

In general, rather more of the activity time occurs before noon than after. The percentages for the seasons 1948–1952 were 65, 60, 75, 60 and 60, respectively.

Behaviour after the Day's Activity.

Logically, the next step should be to deal with variation of population during the day's activity but this will be facilitated by looking first at what the beetles do between the end of one day's activity and the beginning of the next day's.

For about the first week of the flight season *all* the beetles go back into the grass sward after their daily activity, and are thus hidden from view until they emerge into activity again next day. They just disappear into the turf wherever they happen to be when their activity is over. This occurred for the first 7 days in 1948, and for the first 10, 5, 8 and 8 days, respectively, in the succeeding years up to 1952 (mean, 7·6 days).

After the first week, however, a growing fraction of each day's active population spends the whole of the night in full view. Of the latter beetles, the great majority perch on the upper fronds of the fringing bracken (C, figs. 1 & 3). The remainder either stay on the surface of the grassy arena or go right over the bracken fringe to roost on the hawthorn hedge and trees behind (E, figs. 1 & 3). All these "dormitories"—sward surface, hedge and trees, bracken fringe—begin to be used at the same time which is about 3 days before Phase 2 starts (actually 5, 3, 3, 1 and 5 days, respectively, for the successive years 1948–1952). But only one, the bracken fringe, continues to be used right to the end of the flight season.

Passing the night on the surface of the sward always ends when phase-1 activity ends. As an example, peak density of active beetles on the grassy arena each day and the density of beetles remaining on the sward surface at night in 1949 are shown in Table II. The latter density never exceeds 10 per cent. of the former and is usually less.

Roosting on the hawthorn hedge ends simultaneously with that part of phase-2 activity which occurs on the hawthorn (see D & E of fig. 1). Roosting on the hazels and oaks also finishes at that time. This was 14 days before the end of

the flight season in 1949 and 12 days in 1950 (the hedge was cut down in Jan.–Feb. 1951). Resting beetles were very much more numerous on the hawthorn hedge than on the trees.

The bracken fringe is the only " dormitory " used right up to the end of the season. For the latter half of Phase 2, all beetles visible after activity are on the bracken (*cf.* C & E of fig. 1). The population curve of beetles resting nightly on bracken after activity in 1949 is shown in fig. 3 C (*cf.* fig. 3 E).

TABLE II.

Peak numbers of beetles per sq. yd. of grass sward during activity, and numbers per sq. yd. spending the night afterwards resting on the surface of the sward.

	Beetles per sq. yd. on grass sward	
Date	Peak activity during day (38 sq. yd.)	Resting at night (147 sq. yd.)
21 May	P	None
22	P	,,
23	Z	,,
24	Z	,,
25	0·3	,,
26	0·3	,,
27	Z	,,
28	1·4	,,
29	?	,,
30	Z	P
31	2·2	P
1 June	7·4	0·03
2	13·1	0·08
3	Z	Z
4	Z	Z
5	14·7	0·70
6	Z	Z
7	12·0	0·43
8	16·4	1·67
9	8·3	0·40
10	3·3	0·37
11	1·6	?
12	Z	Z
13	0·5	0·03
14	P	P
15	P	0·02
16–28	None	None

Phase 1 ended on 15th June. Data for flight season 1949.

Z = zero activity, *i.e.*, weather so bad that no beetles appeared on the sward surface.
P = some beetles present but too few to be recorded.
? = No counts made though beetles sufficiently numerous to be recorded.

At first, beetles roost on the inner edge of the bracken fringe, *i.e.*, the edge next to the grassy arena—up to a yard in depth where the plants are dense and tall (so forming an abrupt wall) and to 2–4 yards where they are sparse and weak. Numbers fall with distance from the edge. As the season progresses, the beetles penetrate farther and farther into the bracken and concentration on the edge lessens, though it is still discernible even at the end. There is a marked tendency to gregariousness on the bracken. One plant may carry several dozens of beetles while its neighbours show few or none. This clustering effect also lessens somewhat later but again is still quite obvious at the end of the season.

Beetles settle on the upper and lower surfaces of the bracken fronds in about equal numbers, except after a very hot, sunny day (particularly during a droughty spell) when practically all retire to the lower surfaces. During daylight, so long as it is not cold, they cling remarkably to the fronds: the heaviest downpours do not dislodge them, and only the fiercest gale will do so—the latter happened only once in the five years (1950). Nevertheless, if one taps a frond with a finger or even brushes against a bracken plant in walking, the beetles on that frond or plant immediately fall to the ground feigning death.

Between sunset and the start of activity next morning quite an appreciable proportion of the beetle population disappears from the bracken although inactive. The matter was investigated in a total of 94 individuals on 24 bracken plants (1–15 beetles per plant), the work being spread over three different occasions. The initial, *i.e.*, evening, distribution of beetles was: 22 males and 12 females settled on the upper surfaces of the fronds, 37 males and 23 females on lower surfaces. By morning, no beetle had changed its frond, but an equal proportion (34%) of males (20) and of females (12) had disappeared altogether, not only from their respective fronds but also from the plants to which their fronds belonged. Of the 32 vanished beetles, 25 or 78 per cent. had been settled for the night on the lower surfaces of fronds. This and the changed appearance of many of the remaining 62 beetles suggested the cause of the disappearance during the night. In the comparative warmth of the evening, the legs of the beetles had been extended in a firm grip of the frond. Now, in the yet cool conditions of early morning, the legs of most beetles were indrawn (relaxed), several or all of the tarsal claws no longer having a hold; some individuals indeed were lying on their backs, with legs tucked up, on top of fronds close below those to whose lower surfaces they had been clinging on the night before. The latter condition is most evident after a cold, wet, windless night. The colder the night the more common is the relaxing and the greater its degree among beetles. Clearly, the disappearance during the night is caused primarily by a relaxing of hold due to the normal falling of temperature during the night. The proportion of beetles disappearing by night will obviously depend on (a) the position in which beetles settle initially, (b) the amount of temperature fall, and (c) the strength of wind. Thus, if there is no wind, loss of hold will still leave a beetle resting on a surface which is not too much inclined to the horizontal; but, unless at least one claw is caught in plant hairs and/or another frond presses supportingly on the back (a situation often chosen), then the beetle on a steeply sloping upper surface or on a lower

TABLE III.

Evening densities of resting beetles per sq. yd. on the bracken fringe in series of consecutive days.

Starting on	Beetles per sq. yd.				
	1st day	2nd day	3rd day	4th day	5th day
3.vi.52 ..	0·23	*0·05*	0·36	—	—
16.vi.51 ..	2·3	*1·3*	11·0	—	—
19.vi.51 ..	17·7	*5·3*	31·7	—	—
2.vi.49 ..	1·2	*0·2*	*0·0*	1·4	—
25.vi.51 ..	5·5	*4·0*	*2·2*	3·0	—
15.vi.50 ..	8·2	*1·5*	*0·0*	*0·0*	10·3

The same 6 fixed square yards comprised the sample in every case. Beetles counted at 6–8 p.m., *i.e.*, outside the possible daily activity period. The densities in italics were preceded by no activity on that day, due to weather.

surface will drop off to the ground. The more wind and the colder it is, the more beetles will disappear in this way. Never less than 15 per cent. and anything up to 90 per cent. or more of beetles drop off in the night after a day of activity. If one or more days of inactivity supervene, so that no replenishment of roosters is possible, then the entire population may disappear from the bracken within 48 hours (Table III).

The beetles begin to feed when they stop spending the night below the surface of the sward. During the daily activity period beetles generally do not feed, although an odd beetle may be found nibbling the flowers of a herb towards the end of Phase 1 or chewing a bracken frondlet in Phase 2, but these are exceptions to the rule. They generally feed for a few hours after their daily activity finishes (at the very latest, up to 8 p.m.) and a very small proportion of individuals may do so for a few minutes just before activity re-starts next morning. Since they eat what is below their feet, they scarcely move at all when feeding—two or three steps at most. Their food is the living plant substance on which they happen to have come to rest at the end of their day's activity: bracken fronds; blossoms, fruits and leaves of hawthorn; leaves of trees such as oak and hazel; blades of grass; leaves and flowers of herbs, even including nettles, etc., etc.; in fact anything on which they happen to have alighted. Nevertheless, they seem to discern edible matter, for they never come to rest on the bark of branches or trunks of trees, nor on fence posts or rocks. In very hot weather the beetles drink from dewdrops or raindrops encountered on fronds, leaves, etc.

The Diurnal Curve of Population Activity.

In the course of the active period of any day in Phase 1, beetle numbers rise and fall over the grass sward. When weather is uniformly favourable throughout

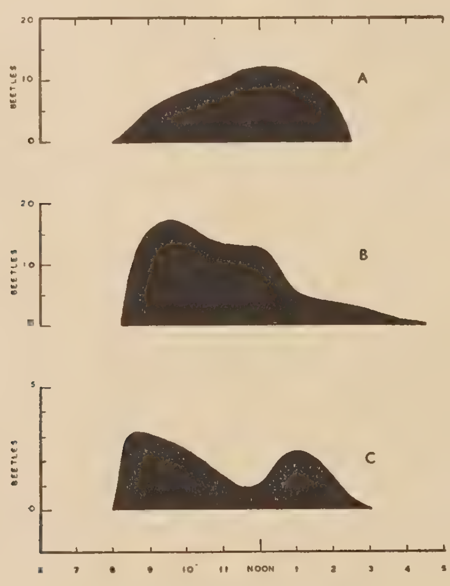

Fig 5.—Examples of diurnal curves of population activity (average densities of beetles active per sq. yd.). A, 7th June; B, 8th June; C, 10th June.

the period, numbers rise sharply to a peak within an hour or two at most, then tail off gradually (*e.g.*, 8th June, fig. 5, B). On the other hand, when conditions are poor to start with but improve steadily as the day goes on, the curve has the opposite form, *i.e.*, with the peak nearer the end than the start of the active period (*e.g.*, 7th June, fig. 5, A). And, of course, when weather vacillates sufficiently the curve is correspondingly irregular: for instance it may have two peaks (*e.g.*, 10th June, fig. 5, C) because some of the beetles return into the sward between the times of these peaks; again, if the weather becomes completely unfavourable for long enough intervals after activity starts in the morning, all the beetles disappear into the sward during those intervals and the result is two or even three separate successive curves during the day.

The daily curve in numbers of beetles active over the grass sward in Phase 1 is governed by the flow of individuals in and out of the turf and to and from the fringing bracken (and trees). The curve, of course, rises when more individuals are arriving than leaving, and falls when the reverse is the case. The traffic in and out of the turf continues right through Phase 1. Indeed there is no other for about the first seven days of the season (see p. 693). After that, however, a growing part of the traffic comes and goes from the bracken fringe. Thus (as noted earlier) for about the next three days some of the beetles do not disappear into the sward at the end of activity but go to the bracken, where they remain all night and return to activity over the sward next morning (*cf.* A, B & C in fig. 1). Then Phase 2 starts and henceforth there is a traffic of beetles to and from the bracken fringe, not only at the beginning and end of the day's activity, but also during it. As Phase 1 wanes, more and more beetles leave the sward during activity to join the busy throng on the bracken. The culmination of this trend may be illustrated from counts made on 15th June 1949, the last day of Phase 1 for that year. It was hot and sunny all day and activity was continuous from 8 a.m. to 3.15 p.m. From the peak at 9.30 a.m. beetle density had fallen by nearly 70 per cent. at 2 p.m. on the grass sward, but in the same time had risen by nearly 240 per cent. on the bracken fringe.

On the bracken fringe, Phase 2, the daily course of numbers is somewhat different from that on the grass sward. For one thing, beetles active on the bracken never disappear when unfavourable conditions intervene between 8 a.m. and 4 p.m.; they merely settle down immobile on the fronds until the weather improves. Again, in the earlier stages of Phase 2, numbers always drop for some little time after activity starts in the morning, and then rise as the day goes on. About 2 p.m. a maximum of numbers is reached and that is maintained until activity is finished for the day and all individuals present settle down to feed and rest on the bracken. For example, there may be 11 beetles per sq. yd. of bracken when activity starts, dropping in about an hour to 5/sq. yd., rising to 13/sq. yd. by noon and to 18/sq. yd. by mid-afternoon, with 18/sq. yd. resting in the evening.

The initial drop and subsequent rise in numbers on the bracken is, of course, caused by differential departure and arrival rates of beetles. In the early days of Phase 2, Phase 1 is still substantial, and some of the beetles spending the night on the bracken return to activity over the grass sward while some of those spending the night on or in the grass sward join the activity on the bracken. The former trend wanes and the latter grows as the day progresses.

As Phase 1 gives way more and more to Phase 2, the initial morning drop fades and the maximum is reached earlier on the bracken. In Phase 2, however, the maximum is always after noon (1 p.m. at earliest) except towards the end, in contrast to Phase 1 with peak generally at or before noon.

Every day throughout Phase 2, until its end, some beetles are arriving on the bracken fringe while others are leaving it, during the activity period. Of those leaving before the end of Phase 1 some are bee-liners, and after the end of Phase 1 practically all are bee-liners.

Behaviour in the Absence of Bracken and Hedges.

Target Field, Rydal, is a heavily infested *Agrostis-Festuca* pasture of about 40 acres. Except for a high knoll covering about 6 acres in the centre and a rising at the edge on three sides, the field is flat. It contains no bracken and has no surrounding hedge. But tall deciduous trees on the central knoll and bordering the field are utilised in exactly the same manner as the bracken fringe of U.H.H.F., Buttermere. The beetles carry out their phase-2 activity on those trees nearest to where they emerged on the grass sward. They can be seen flying, mating, feeding and resting from top to bottom of the trees, which are 50–60 ft. or more high. The few conifers present are completely avoided.

The knoll trees, being as it were on a small island in the middle of the expanse of grass sward, are excellent for the study of bee-liners (see later papers).

Summary.

Previous descriptions of the flight season of the Garden Chafer, *Phyllopertha horticola* (L.), are inadequate. From a study of five seasons, 1948–1952, the general or mass aspects may be outlined for the English Lake District as follows:—

The flight season starts in May or June, depending on soil temperature. When population is low the season lasts 3–4 weeks, when high it may last 5–6 weeks. Reasons for this are given.

The flight season has two overlapping phases. In Phase 1, beetles swarm close over the grass sward from which they emerged. As the season progresses, Phase 1 gradually gives way to Phase 2, in which the beetles now swarm closely on the bracken, hedges and trees surrounding the pasture. In the absence of bracken, the whole of Phase 2 takes place on hedges and/or trees. In the presence of bracken, phase-2 activity at first occurs on all three (bracken, hedges and trees) but, for some obscure reason, hedges and trees are forsaken in favour of bracken about halfway through the phase. Roughly speaking, phase-1 activity can be seen for the first two-thirds and Phase 2 for the last two-thirds of the flight season, *i.e.*, there is about 50 per cent. overlap of the phases. The overlap is clearly due to earlier-emerging beetles entering phase-2 activity before later beetles have completed Phase 1.

Normal activity (*i.e.*, flying closely over, or running or walking upon, the vegetation) is governed by weather. Both temperature and light are involved. Beetles are most active in warm bright conditions and, indeed, will fly and run only when the sun is shining. In warm bright-overcast conditions, they merely walk around. In cold, dull-overcast conditions (with or without wind or rain), they do not stir at all.

Activity starts any time between 8 a.m. and 2 p.m. (G.M.T.) according to weather (earliest recorded start being 7 a.m.). The first day of the flight season is usually marked by a short period of activity, 1–2 hours, in the forenoon, even when weather conditions continue favourable into late afternoon. As the days pass the period lengthens until beetles are active up to about 4 p.m. (latest recorded finish being 4.30 p.m.). The longest periods of activity, 8 a.m. to 4 p.m., occur when the sun shines all day after the first week of the season has passed. As the season draws to an end the activity period shortens until on the last day it is one hour or less. In general, rather more of the activity time occurs before noon than after.

The curve of numbers of beetles to be seen during the daily activity period is described for both phases. During the time of overlap of the phases, the curves are complicated by a certain amount of two-way traffic between grass sward and bracken (or hedges or trees). In addition, throughout Phase 2 a small proportion of individuals leaves the bracken flying high, straight and very fast, *i.e.*, behaves abnormally; these individuals are termed "bee-liners" and will figure in a later paper.

For about the first week of the flight season all beetles disappear into the sward at the end of the day's activity. After that, a growing fraction of each day's active population spends the whole night in full view on the sward surface, bracken fringe, hedges and trees. All these "dormitories" begin to be used at the same time, *i.e.*, about three days before Phase 2 starts. Passing the night on the sward surface ends with Phase 1. Roosting on hedges and trees ends simultaneously with activity there (first half of Phase 2). The bracken fringe alone is used right to the end of the season. Between sunset and sunrise, from 15 to 90 per cent. or more of resting beetles fall from bracken, hedges or trees to the ground. Reasons for this are given.

Beetles begin to feed when they stop spending the night below the sward surface. They feed after the day's activity is finished, and up to 8 p.m. at the latest. Their food is the herbage, bracken frondlets, leaves, blossoms, fruits, etc., on which they come to rest for the night.

Acknowledgements.

Thanks are due to Messrs. T. P. McNicol and R. Coggins for help in the field, and to Mr. R. Laughlin for constructive criticism of the manuscript.

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EFFECTS OF THE ANT, *LASIUS NIGER* (L.), ON THE BEHAVIOUR AND REPRODUCTION OF THE BLACK BEAN APHID, *APHIS FABAE* SCOP.

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Many observers have recorded that populations of Aphids and Coccids, visited by ants for the honeydew they excrete, multiply more rapidly than those not attended by ants (Nixon, 1951; Flanders, 1951). Several explanations have been advanced: ants give different degrees of protection against the natural enemies of the Homoptera; the colonies are "healthier" because the ants remove exuviae and the sticky honeydew; the ants sometimes transport the Aphids or Coccids to favourable feeding sites where their nutrition is improved.

Some Homoptera are unable to survive without attendant ants because they become immobilised and are killed in the accumulated honeydew in which fungal parasites of the insects may develop, and because of attacks by insect enemies (Way, 1954). Like many other Homoptera, *Aphis fabae* Scop. usually colonises its various host-plants very successfully without being attended by ants. This Aphid ejects its honeydew forcibly and easily and this, therefore, does not accumulate and kill the insects.

A. fabae on beans is occasionally visited and attended by the ant, *Lasius niger* (L.), and such colonies are said to benefit from the consequent protection from insect enemies, and possibly from a direct effect which the ant has in stimulating the Aphid's excretion rate. Herzig (1937) believed that there is, therefore, an increased absorption of plant sap and consequently a higher rate of reproduction. El-Ziady & Kennedy (1956) concluded from experiments that, whether predators were present or not, the ant, *L. niger*, increased the rate of multiplication of *A. fabae* and delayed the production of winged forms, and they suggested that the ant might raise the "plane of nutrition" of the Aphids. They considered that the protection of the Aphids against attacks by insect enemies was perhaps of secondary importance.

The object of the work described below was to assess the effect of the ant, *L. niger*, on the reproduction rate of *A. fabae* on broad beans (*Vicia faba*) in the absence of the Aphid's insect enemies under experimental conditions; and to reconsider the manner in which this effect is brought about.

Methods.

The experiments were carried out in a garden where natural nests of the ant, *L. niger*, were common under paving stones. Single bean plants in 5-inch flower pots were infested with *A. fabae* from a stock culture and were placed in large insect-proof cages in the garden close to the ants' nests. The cages (3 ft. × 2 ft. × 2 ft.) were of wood with the door and rear panel fitted with glass, the sides and top being of fine muslin. Some of the cages, all of which were raised above ground on up-turned flower pots, were made ant-proof by smearing the insides and outsides of the supporting pots with a ring of tree-banding grease.

Ants were established in the other cages in the following way before experiments started. Large numbers of ants were collected from under the paving stones with an aspirator attached to an electrically-driven vacuum pump, the

strong draught of air through the apparatus preventing the insects from killing themselves with their own vapour. The ants were then tipped from the aspirator on to the leaves of aphid-infested plants in the cage; some of the ants settled at once to tend the Aphids but the majority ran off the plants and eventually found their way out of the cage through a hole in the floor. Drops of honey on the inside of a supporting pot and on the floor of the cage encouraged the ants to enter and form a trail to and from the nest by way of the hole in the floor. In this way Aphids on all plants were usually tended successfully by ants within 24 hours.

When an experiment was to be started, the ants already tending the Aphids in a cage were removed with an aspirator and transferred individually to the experimental plants which had been put into the cage to replace the previous plants. This method of establishing ants with the aphid colonies was usually successful but on several occasions ants left the plants during the course of experiments which had then to be abandoned.

The experimental plants were infested with apterous nymphs of *A. fabae* taken from a stock culture kept in insect-proof cages in a glasshouse. These Aphids were the progeny of alatae feeding and reproducing on young bean plants and had not previously been ant-attended. Young apterous nymphs (2nd and 3rd instars) were picked off the stock plants with brushes and transferred individually to the apical leaves of the experimental plants; alternatively, groups of these nymphs were transferred on a section of leaf. Aphids were allowed to settle on their new plants overnight before use.

During the experiments, the plants in the cages were examined at least once, sometimes twice, daily and the numbers of attendant ants recorded. Cages were examined carefully for any predators, especially for Anthocorid nymphs whose small size allows them to enter where larger predators cannot pass. The plants were watered frequently to prevent wilting in hot weather.

In the experiments, 6, 7, 8 or 12 plants were used in each cage at a time and from them, at various times, 3 or 4 sample plants were taken at random from both kinds of cage for counting of Aphids.

Sample plants were cut up and preserved immediately in 90 per cent. alcohol and the Aphids sorted and counted later; in this way no Aphids were lost. Inspection of the plants with a hand lens to count Aphids *in situ* is usually inaccurate (except when Aphids are few), because many small nymphs cannot be seen unless leaflets are pulled to pieces and the Aphids washed out from the crevices.

Experiments on the reproduction rates of individual Aphids were carried out in an insectary during the summer. Aphids were confined to mature leaves or to the bunch of apical leaflets of potted bean plants in transparent plastic cages, 3 in. × $1\frac{1}{2}$ in. × $\frac{1}{2}$ in. Each cage was supported by a wire frame clipped to an upright stick; a hole in the base of the cage surrounded the leaf petiole or stem and a plug of cotton-wool prevented Aphids and other insects from crawling in or out. A rectangular hole, cut in the sliding lid and in the bottom of each cage, was covered with fine muslin to provide ventilation.

Behaviour of *L. niger* and of *A. fabae*.

Smith (1937) described the act of excretion in *Hyalopterus pruni* (Geoffr.) and Broadbent (1951) amplified Smith's description for that and other aphid species. The nymph of *A. fabae* raises the abdomen so that the body is almost at right angles to the leaf or stem surface, the stylets remaining inserted in the plant tissue. One or both hind legs are waved once or twice and the Aphid swings its raised abdomen from side to side. The abdomen may then be lowered and the performance repeated before a clear transparent droplet of honeydew appears at

the anus. As the droplet emerges, one of the hind legs is flexed at the femoro-tibial joint and, as the globule reaches its full size, the leg is suddenly straightened to flick the globule off the anus.

In adult apterae the same preliminary restlessness occurs before excretion, but the hind legs are not always raised from the plant surface. As the globule appears, the cauda is flexed forward dorsally and is suddenly jerked backwards to flick off the globule when it has reached its maximum size. In both nymphs and apterae the globule is thrown for a considerable distance and Smith commented on the uniformity of the force and direction of the throw. Adult Aphids produce larger droplets but excrete less frequently than nymphs.

A foraging ant approaches and palpates the abdomens of the nearest Aphids with the tips of its antennae. An Aphid responds immediately by raising its abdomen slightly and at the same time emitting the honeydew; but the hind legs are often not moved off the plant surface and if raised at all are not waved in the usual manner.

The ant responds by taking the drop of honeydew between its jaws, the labial palps and sometimes the antennae themselves manipulating the droplet into the mouth. Globules occasionally become stuck to the ant's antennae.

An ant usually palpates more than one Aphid at a time; while it is taking honeydew from one Aphid, another, also having honeydew to give, will withdraw the globule into the anus and lower its abdomen, raising it and offering the honeydew once more when it is again palpated.

When the ant is replete its gaster becomes distended. It wanders away from the Aphids, occasionally returning to them several times but eventually leaves them and moves rapidly down the plant towards the nest. Replete ants returning to the nest move much faster than those coming from the nest to the Aphids and they rarely hesitate or deviate from their normal route.

An ant will repeatedly palpate all the Aphids of a group although it may receive no more honeydew from some of them. It appears that the honeydew supply of these Aphids is temporarily exhausted and that they need time to recover. If there be few Aphids in a group the ant may be unable to fill itself, whereupon it may leave them to visit another colony or sometimes to return at once to the nest.

When the ant has departed, the Aphids remain motionless and do not emit any honeydew; but they become restless after a time and wave their abdomens and legs as if ready to excrete. After an average time of 20 min. one or two of them emit droplets which are often conspicuously larger than those they produced before the ant attended them; but even 1 hr. after the ant has left, the rate of extrusion is still less than it was before the Aphids were attended.

The normal excretion behaviour of the Aphid is altered when attended by ants, therefore, in several ways: the hind legs are not waved; they are often not lifted and the abdomen is raised only slightly, not at right angles to the plant; Aphids often withdraw the honeydew into the anus if the ant does not take the globule; Aphids which have been ant-attended are able apparently to store their excreta for a short time until the ant returns. The absence of honeydew from the leaves of ant-visited plants (p. 707) supports this view.

Dispersal of Aphids over Bean Plants.

A typical natural infestation by *A. fabae* in the crown of leaflets of a bean plant is the progeny of one or more adult alatae which settled there. The nymphs remain clustered around the parent, feeding on and between the young unfurled leaflets, in the folds of which many of them are hidden. As the leaflets grow, they unfurl and expand, exposing the Aphids which soon move on to more unfurled leaflets at the top of the plant; the process is later repeated.

TABLE I.

Distribution of total apterae (a) and nymphs (n) on 6 ant-visited (A) and 6 ant-free plants (B) on three occasions. The first mature leaf is the basal and oldest.

Day of experiment	No. of sample plants		Mature leaves														Apical leaflets and top of stem		Total		Apterae at tops of plants	Total Aphids at tops of plants
			1st		2nd		3rd		4th		5th		6th		7th							
			a.	n.	a.	n.	a.	n.	a.	n.	a.	n.	a.	n.	a.	n.	a.	n.	a.	n.	(%)	(%)
11th	6*	A	0	0	1	1	0	1	0	1	7	48	–	–	–	–	62	529	70	580	89	91
(time t_1)	6*	B	10	120	4	31	3	20	2	37	2	0	–	–	–	–	35	175	56	383	63	48
19th	3	A	0	0	0	1	2	16	3	25	1	3	4	38	6	58	200	1812	216	1953	93	93
(time t_2)	3	B	9	219	1	8	2	80	13	71	4	67	3	2	0	55	94	865	126	1367	75	64
24th	3	A	10	49	10	141	17	231	33	443	40	351	3	139	–	–	148	3874	261	5228	57	73
(time t_3)	3	B	25	228	25	156	12	113	13	77	14	236	0	22	–	–	88	2158	177	2990	50	71

* Aphids on all plants counted *in situ*; no sample plants removed from cages.

The Aphids grow and become apterae whose progeny enlarge the colony which consists of Aphids in all stages of growth, nymphs always being more numerous than apterae; alate nymphs do not usually appear until late in the infestation. The apex of the plant soon becomes overcrowded and the colony gradually occupies more and more of the stem. At an early stage of the infestation some apterae move away from the apical colony to settle on and colonise the under-surfaces of fully expanded, mature leaves lower down on the plants. Ibbotson & Kennedy (1950) showed how the spread of colonies of *A. fabae* on sugar-beet plants is caused mainly by adult apterae whose feeding preferences largely determine the general pattern of the infestation. The actively growing and senescing leaves were more susceptible to colonisation by apterae than the mature and dying leaves (Kennedy, Ibbotson & Booth, 1950). Apterae of *A. fabae* on bean plants show a similar preference for the very young and old leaves. As a plant grows and ages, more and more leaves become colonised.

To simulate the natural process, young apterous nymphs were transferred to the apical leaflets of the experimental plants; the development of these colonies and the dispersal of the apterae were similar to those of natural infestations.

Effects of Ant-attendance on Aphid Dispersal.

When ants attend *A. fabae* on bean plants, the dispersal of apterae from the initial apical colonies is noticeably delayed, so that the Aphids remain aggregated in dense colonies at the tops of the plants for a considerable time. This delay, which was observed in all the experiments, is illustrated by the events of the following typical experiment (Experiment 3 of Tables II and III).

Twelve young bean plants, 8 in. high, were infested each with 16 small apterous nymphs and set up in two equal batches in separate cages. In one cage (A) ants were established and from the other (B) ants were excluded.

After 11 days (time t_1), those Aphids that could be seen on all plants were counted carefully *in situ* with a lens and the distribution of apterae and nymphs recorded (Table I). In cage A, 91 per cent. of the Aphids were concentrated among the apical leaflets and at the tops of the stems in dense compact colonies; only 9 per cent. were on mature leaves. In cage B, however, only 48 per cent. of the Aphids were at the tops of the plants while more than half of them were scattered in numerous small colonies over the leaves, the majority of them being on the lowest (oldest) leaves. The ant-attended Aphids were nearly 50 per cent. more numerous than the ant-free. Of the apterae, 89 per cent. in cage A and 63 per cent. in cage B were on the young apical growth.

Thus, at this early stage of the experiment, many of the ant-free apterae had left the apical colonies and settled on old leaves, whereas nearly all the ant-attended apterae had remained in the dense colonies at the tops of the plants.

Although the Aphids in cage A continued to increase and the colonies to enlarge, no apterae crawled away from the tops of the plants during the next seven days; nor did any apterae crawl off the plants in cage B. On the 19th day of the experiment (time t_2), only one day later, large numbers of apterae were found crawling on the walls of cage A; some of them had settled and reproduced on the lower leaves of the plants where ants continued to attend them; in cage B there were still no such crawling Aphids. A sample of three plants from each cage showed that in cage A most of the Aphids (93%) and of the apterae (93%) were situated, as before, at the tops of the plants, although many apterae had moved away. In cage B, 64 per cent. of all Aphids and 75 per cent. of apterae were at the tops of the plants, the remainder being dispersed over the leaves.

Apterae continued to move off the plants in cage A and some appeared off the plants in cage B during the next five days but the numbers in A (340) far exceeded those in B (191) (see fig. 1).

On the 24th day of the experiment (time t_3), only 57 per cent. of apterae and 73 per cent. of all Aphids in cage A were situated at the tops of the plants: the proportions there had become similar to those in cage B (50% apterae and 71% of all Aphids); but total ant-attended Aphids exceeded ant-free Aphids by 73 per cent. The rapid increase in the proportion of ant-attended Aphids on lower (mature) leaves as crawling apterae colonised them is shown in fig. 1.

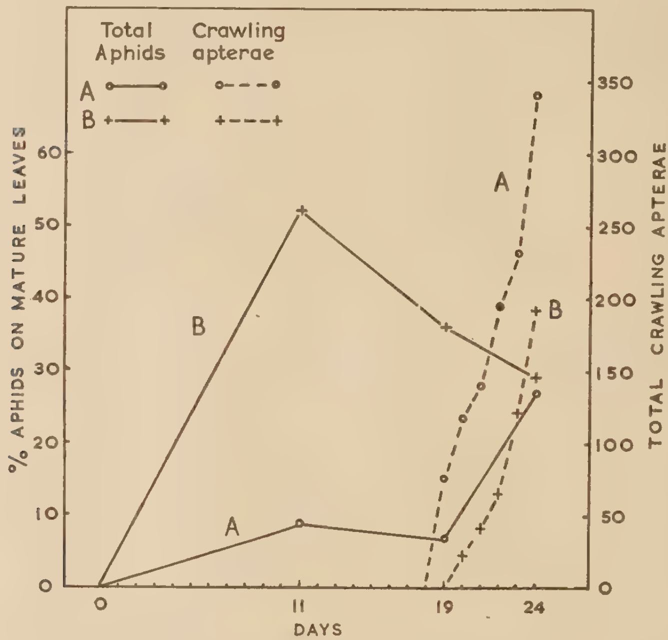

Fig. 1.—Experiment 3. Changes in proportions of total Aphids on the mature leaves of ant-visited (A) and ant-free (B) bean plants. The numbers of crawling apterae in the cages are also shown.

Ant-attendance had, therefore, the outstanding effect of delaying the dispersal of the apterae from the apices of the plants; but it did not prevent dispersal. The apterae eventually scattered, some of them settling and reproducing on old leaves; but many of them left the plants altogether so that they no longer contributed to the growth of the aphid populations.

Effects of Ant-attendance on Aphid Multiplication.

During the summers of 1956 and 1957, six experiments were carried out to assess the increase in numbers of ant-attended Aphids in the absence of enemies.

In each experiment, potted bean plants, infested with equal numbers of young apterous aphid nymphs, were placed in two insect-proof cages sited in the open under similar conditions of daylight, temperature and wind. Ants, *L. niger*, were established on the plants of one cage and the control plants were isolated from ants.

The initial numbers of Aphids per plant and the number of plants per cage differed from one experiment to another. In four of the experiments, two sets of samples were taken; an earlier one (at time t_1) between 7 and 13 days from the start of the experiment, before or just after some of the apterae had crawled

off the plants; and a later set (at time t_2) when many apterae had dispersed over the ant-visited plants. In two experiments, samples were taken on only one occasion; in Experiment 3, counts were made on three occasions as previously described.

In all experiments, moulds and bacteria developed on the honeydew which accumulated on many of the lower leaves of the ant-free plants; aphid exuviae and dust also stuck to the upper surfaces of these leaves. The intensity of fungal development depended on the degree of scattering of the Aphids and on their numbers. After two to three weeks, many of the leaves had well-developed patches of fungi which sometimes severely damaged them. In contrast, ant-visited plants were kept free of honeydew so that no fungi developed on the leaves unless Aphids became so numerous that the attendant ants were unable to cope with the excreta. Other ants from the nests, not aphid-tenders, were attracted and fed on the droplets on the leaves.

TABLE II.

Effect of ant-attendance on aphid multiplication.

Experiment	Initial no. of Aphids per plant	Sampling occasion	No. of samples	Day of experiment when samples taken	Total Aphids on samples: Ant-attended (A)	Total Aphids on samples: Ant-free (B)	Difference (A > B) (%)
1 ..	23	t_1	4	13	914	706	29·5
2a ..	63	—	3	7	2697	2521	7·0
2b ..	63	—	3	7	3212	2521	27·4
3 ..	16	—	6*	11	650	439	48·1
4 ..	16	—	4	7	2785	2158	29·1
5 ..	16	—	4	7	894	582	53·6
1 ..	—	t_2	4	37	4447	3886	14·4
2a ..	—	—	4	12	5098	4250	20·0
2b ..	—	—	4	12	5630	4250	32·5
3 ..	—	—	3	19	2207	1493	47·8
3 ..	—	t_3	3	24	5805	3424	69·5

* Aphids on all plants counted *in situ*; no sample plants removed from cages.

The totals of Aphids on the ant-visited plants always exceeded those of the ant-free plants, whenever the time of sampling (Table II). The excess varied from 7 to 70 per cent. and averaged 31 per cent.

This increased multiplication of the Aphids is indicated (with one exception) by the higher ratio nymphs/apterae on the ant-visited plants during the early stages of the experiments (at t_1, Table III). Because many apterae crawled off the plants later in the experiments, this ratio was then no longer so useful as an index of the reproduction rate of the Aphids.

At t_1, very few alatae (adult alatae plus 3rd- and 4th-instar alate nymphs) had appeared, but in all the experiments there was a slightly higher proportion of alatae on the ant-free plants. At t_2, the proportions were sometimes higher on the ant-visited plants (Table III).

Experiment 3 has already been described. Of the others, only experiments 2a and 2b deserve special comment. They were carried out simultaneously, one cage (B) without ants acting as control to the two with ants (A_1 and A_2). There were nearly twice as many ants on the plants in cage A_1 as in

TABLE III.

Comparisons of numbers of apterae, ratios of nymphs/apterae and proportions of alatae on ant-visited (A) and ant-free plants (B).

Experiment	t_1						t_2						t_3					
	Total apterae on the plants		Nymphs/apterae		Alate Aphids (%)*		Total apterae on the plants		Nymphs/apterae		Alate Aphids (%)		Total apterae on the plants		Nymphs/apterae		Alate Aphids (%)	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
1	73	64	11·5	10·0	8·0	9·1	103	44	42·1	87·3	2·7	1·3	—	—	—	—	—	—
2a	123	166	20·7	13·9	5·5	8·7	85	165	58·5	24·3	2·4	5·7	—	—	—	—	—	—
2b	109	166	28·3	13·9	4·0	8·7	67	165	82·4	24·3	1·8	5·7	—	—	—	—	—	—
3	70	56	8·3	6·8	0	0	216	126	9·0	10·8	3·2	1·9	261	177	20·0	16·9	9·0	10·7
4	109	93	23·8	22·0	2·2	2·5	—	—	—	—	—	—	—	—	—	—	—	—
5	71	28	11·6	19·8	4·1	6·9	—	—	—	—	—	—	—	—	—	—	—	—

* The detailed figures from which these percentages have been derived have been omitted.

cage A_2. In each cage, seven plants were infested with 63 nymphs and, because of this high initial number, apterae scattered very early in all the cages, especially in the ant-free cage where the crawling apterae were much more numerous than in the other two cages.

A set of three sample plants was taken from each cage on the 7th day of the experiments (Table IV). The delay in dispersal of the ant-attended apterae is indicated by the lower numbers of crawling apterae in cages A_1 and A_2. In the cage with fewer ants (A_2), the total aphid population and the reproduction rate of the apterae (ratio nymphs/apterae) were higher than those of cage A_1 although in A_2 the apterae were fewer.

After the removal of the samples, the ants became more abundant on the remaining plants but they were in approximately the same ratio as before. The results when the experiments were finished on the 12th day are also summarised in Table IV. A higher percentage of apterae had left the plants in cage A_2 (with the fewer ants) but, despite the small numbers of apterae, the reproduction rate and the total aphid population there, were still the highest.

These results suggest that the size reached by a population of Aphids might be associated with the numbers of attendant ants, but further research is needed for more convincing evidence.

Reproduction of Individual Aphids.

Kennedy & Booth (1954, p. 97) showed that apterae of *A. fabae*, when transferred to plants of sugar-beet and spindle (*Euonymus europaeus*), preferred to settle on young leaves rather than old leaves and that they produced 50 to 100 per cent. more nymphs on the young than on the old. The effect of age of leaf (nutrients) on the reproduction rate of the Aphid was emphasised.

El-Ziady & Kennedy (1956) suggested that ant-attendance might cause a direct stimulation of the feeding of the Aphid which might raise its "plane of nutrition" and hence its reproduction rate.

In the present work, most of the ant-attended Aphids remained on the apical growth of the bean plants for a longer period than the ant-free Aphids, many of which settled on the old leaves. It seemed probable, therefore, that the indirect effect of the ants in keeping the Aphids concentrated on the young growth of the plants might be as important as any direct effect of ant-attendance. Experiments were made, therefore, to see if any such differences exist between Aphids previously ant-attended and ant-free, respectively, and between Aphids living on young and old leaves of bean plants.

Experiment I.

Twelve crawling apterae were taken at random from one of the ant-free experimental cages and transferred in pairs to three young leaves and to three old leaves of separate bean plants. The Aphids were confined to the leaves in small plastic cages which were dismantled after six days, before the next generation of adult Aphids appeared.

On the young leaves, each aptera produced an average of $35 \cdot 5 \pm 2 \cdot 0$ nymphs, which was 42 per cent. more than the mean of $25 \cdot 0 \pm 0 \cdot 4$ nymphs produced in the same time on the old leaves. The difference was significant ($P = 0 \cdot 05$).

Experiment II.

Twelve last-stage apterous nymphs (attended by ants from birth) from the apical growth of ant-visited plants and twelve similar nymphs from the tops of ant-free plants were transferred in pairs to young leaves and to old leaves of separate bean plants and were confined in the plastic cages. After six days of reproduction by the apterae, the cages were dismantled and the Aphids counted.

TABLE IV.

Summary of experiments 2a and 2b in which the numbers of two sets of Aphids (A_1 & A_2), attended by different numbers of ants, were compared with the numbers of ant-free Aphids of a control (B) on two occasions.

Day of sampling	Cage	No. of sample plants	No. of ants per plant	Apterae On plants	Apterae Crawling	Nymphs	Total Aphids of the samples	Apterae (%)	Crawling apterae (%)	Nymphs/apterae
7th	A_1	3	8·3	123	24	2550	2697	5·5	16·3	20·7
	A_2	3	4·7	109	19	3084	3212	4·0	14·8	28·3
	B	3	0	166	54	2301	2521	8·7	24·5	13·9
12th	A_1	4	14·5	85	35	4974	5098	2·4	29·2	58·5
	A_2	4	9·5	67	36	5523	5630	1·8	35·0	82·4
	B	4	0	165	79	4003	4250	5·7	32·4	24·3

The numbers of young produced by the Aphids which previously had been ant-attended did not differ significantly from the numbers produced by those that had not; nor were there any significant differences between the numbers of nymphs born on young and old leaves. Contrary to expectation, there was a tendency for the ant-free Aphids to produce more nymphs (6 and 13%) than the ant-attended Aphids; in contrast, there was a tendency towards more nymphs (19 and 27%) on young leaves than on old leaves (Table V).

TABLE V.

Effect of age of leaf on the mean number of nymphs produced by apterae from ant-visited (A) and ant-free (B) bean plants when transferred as last-stage nymphs to fresh ant-free bean plants.

Experiment II		(A)	(B)	Difference (%) (B > A)
Transferred from young growth to :	Young leaves (Y)	13·5 ± 1·2	14·3 ± 1·5	6
	Old leaves (O)	10·7 ± 1·9	12·0 ± 1·3	13
	Difference (%) (Y>O)	27	19	

Experiment IV		
	(A) young leaves	(B) young leaves
Transferred from young growth to :	36·6 ± 2·1 (a)	38·0 ± 2·8 (b)
	(B) young leaves	(B) old leaves
Transferred from old leaves to :	32·2 ± 1·5 (c)	28·2 ± 2·0 (d)

a–b, $P > 0{\cdot}10$ (not significant)
b–c, $P = 0{\cdot}10$ (barely significant)
b–d, $P = 0{\cdot}02$ (significant)

Experiment III.

Fifteen apterous nymphs that had been ant-attended since birth, and 15 apterous nymphs that had not, all in the last instar, were transferred from the tops of bean plants to separate bean seedlings, one inch high, so that only very young plant growth was available to the Aphids.

After nine days, the 15 apterae which had been ant-attended as nymphs, had produced 299 nymphs; the 15 control apterae had produced 310 nymphs in the same time. The means were almost identical.

Experiment IV.

Six apterous nymphs that had been ant-attended from birth, and 6 apterous nymphs that had not, all in the last instar, taken at random from the *young* growth at the tops of the plants in the experimental cages, were transferred individually to cages on the young growth of fresh bean plants.

At the same time, 12 apterous nymphs were transferred from *old* leaves of ant-free plants to fresh bean plants, 6 being confined individually to young leaves, 6 individually to old leaves. All the Aphids were allowed to mature and to reproduce for six days, when the numbers of nymphs were counted (Table V).

There was no difference of any significance ($P > 0{\cdot}10$) between the numbers of nymphs produced on the young growth by the apterae that had been ant-attended as nymphs and those that had not. Aphids transferred from ant-free young growth to young growth produced significantly more nymphs than those

transferred from old leaves to old leaves ($P = 0{\cdot}02$), and more ($P = 0{\cdot}10$) than those transferred from old leaves to young growth.

Thus, it appears that the reproduction rates of the Aphids are not affected so much by a direct action of ants attending them as by the age of the leaf or part of the plant on which they have developed or are then feeding, that is, by the effect of nutrition.

Discussion.

Quantitative evidence that ant-attended Aphids multiply more rapidly than ant-free Aphids is scarce. The principal evidence is that of Herzig (1937) who, in a summary of conclusions, stated that the multiplication of *A. fabae* and its ability to absorb sap can be doubled or trebled by the attendant ants, *L. niger* and *L. fuliginosus* (Latr.). This conclusion was based on the results of one field experiment (pp. 421–423) in which the Aphids attended by *L. niger* on a bean plot were said to be twice (not thrice) as numerous as those of a control plot. Herzig gave no counts of aphid numbers and he did not exclude predators or parasites from either plot; indeed, he implied that they were present, for he said that the heavier infestation of the ant-visited plants was due partly to the slight protection which the ants gave to the Aphids. The difference in aphid populations of the two plots was probably caused, therefore, by the action of natural enemies on the ant-free plot. Because his other experiments suggested that ant-attended Aphids excrete more honeydew than ant-free Aphids, he assumed that they absorb more plant sap and, therefore, produce more offspring. On pp. 423 and 426 this assumption is presented as a proven fact, which has been quoted by other authors (Nixon, 1951, p. 15; Waterhouse & Day, 1953, p. 334).

El-Ziady & Kennedy (1956) made three experiments to compare the rates of multiplication of ant-attended and ant-free colonies of *A. fabae* on beans. In their first experiment, insect enemies were not excluded and the large difference in aphid numbers is probably to be attributed to predation and parasitism. In the remaining two experiments, from which predators were excluded, ant-attended Aphids were 40 per cent. and 70 per cent. more numerous than ant-free Aphids.

The results of the experiments described above confirm that populations of *A. fabae*, attended by *L. niger*, multiply more rapidly than do those of ant-free Aphids when natural enemies of the Aphid are absent. The average difference in numbers under the conditions of the experiments was about one-third, the maximum being 70 per cent.; no doubling or trebling of aphid numbers, as claimed by Herzig, was ever recorded.

No significant differences were found between the numbers of nymphs produced by individual Aphids that had previously been attended by ants and those produced by ant-free Aphids living on leaves of the same age; but the numbers were significantly affected by the age of the leaf or part of the plant on which the Aphids had developed or were then feeding.

It is suggested that ant-attended colonies increase in size more rapidly because the normal dispersal of apterae from the young apical growth of the bean plants is considerably delayed; the Aphids reproduce more rapidly there, presumably because they obtain a more nutritious food supply for a much longer period than most ant-free Aphids, many of which disperse to older and apparently less nutritious leaves where their reproduction rate is lower. The possibility of a direct effect of the ants on the Aphids is not excluded, but further research is needed to demonstrate its existence.

The main effects which the ant, *L. niger*, has on the behaviour of *A. fabae* are the changes in excretion behaviour reported above and the apparent inhibition, for a time at least, of the tendency of the Aphid to disperse from the apical colonies.

Summary.

Cage experiments confirmed that, in the absence of natural enemies, populations of *Aphis fabae* Scop., attended on bean plants (*Vicia faba*) by the ant, *Lasius niger* (L.), multiply more rapidly than otherwise similar but ant-free populations. The average difference in numbers recorded was about one-third, the maximum being 70 per cent. No doubling or trebling of aphid numbers as claimed by an earlier worker was ever recorded.

When the Aphids are attended by ants, their excretion behaviour alters and the normal dispersal of the apterae from the young apical growth of bean plants is considerably delayed.

No significant differences were found between the numbers of nymphs produced by individual Aphids from ant-visited and ant-free plants, respectively, living on leaves of the same age; but the numbers were significantly affected by the age of the leaf or part of the plant on which the Aphids had developed or were then feeding.

It is suggested that ant-attended aphid populations multiply more rapidly because most of the Aphids feed for a much longer time on young plant tissue where, presumably, their food supply is more nutritious.

Acknowledgements.

I am grateful to Dr. L. Broadbent for reading and commenting on the manuscript of this paper, and to Mr. F. G. Smith, whose help with the experiments was indispensable.

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FIRST RESULTS IN THE CONTROL OF *SIMULIUM DAMNOSUM* THEOBALD (DIPTERA, SIMULIIDAE) IN NORTHERN NIGERIA.

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Surveys for onchocerciasis and *Simulium damnosum* Theo. carried out between 1951 and 1955 showed that the disease and its vector are of widespread distribution in Northern Nigeria, and that in some areas onchocerciasis is a major cause of blindness (Budden, 1955, 1956; Crosskey, 1956). Towards the end of 1954, the Medical Department, as a result of these surveys, became interested in the possibility of establishing a pilot project for the control of *S. damnosum* to assess the prospects for the control of this insect by the larvicidal treatment of its breeding grounds. It was appreciated that such a scheme would be of an experimental nature, since it was desired to put it into operation in an area where a network of non-isolated breeding rivers existed, whereas control of *S. damnosum* had only been attempted elsewhere (Wanson, Courtois & Lebied, 1949, in Belgian Congo, and Barnley, 1953, in Uganda) in isolated, although very large, foci.

Although a number of well isolated foci of *S. damnosum* exist in Northern Nigeria, it was preferred to site the experimental control project in an area comprising a series of non-isolated breeding rivers, *i.e.*, where reinfestation of the cleared rivers was likely to occur, for in general the onchocerciasis problem is most serious in the very large areas where whole river systems are infested, and it is this type of area which will provide the greatest challenge to control.

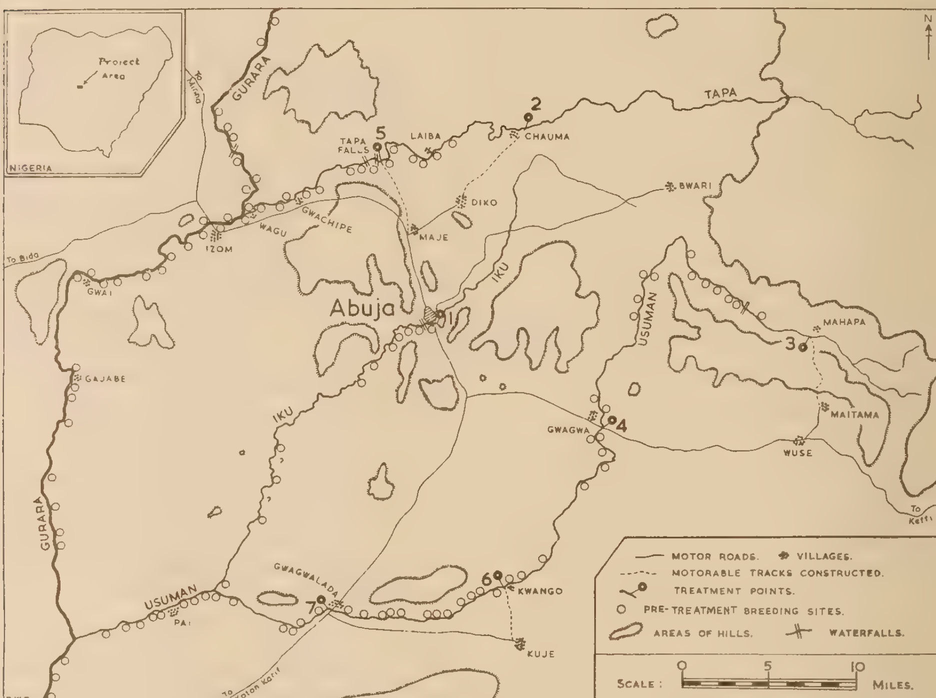
The selection of a suitable area for the control project was rendered difficult by the remoteness and inaccessibility of many of the areas where *S. damnosum* occurs, for it was thought essential that the area should be easily accessible by road at all times of the year. Consideration was given to each of the known foci in Northern Nigeria, and the Abuja area of Niger Province was finally chosen. This area appeared to be the most suitable, as Abuja lies on an all-season road only 70 miles from the provincial headquarters at Minna and the nearest railhead; it further has postal communications, and the area has been accurately mapped on a scale of 1:125,000. The latter consideration was regarded as particularly important as, in most areas of Northern Nigeria, work in the field is severely handicapped by the absence of large-scale or accurate small-scale maps; for although most of the country has now been photographed from the air, maps are not yet available from the aerial survey, and the existing maps generally show the courses of the rivers (with which one is principally concerned in *Simulium* control) quite inaccurately.

Preliminary observations on *S. damnosum* were begun at Abuja in late 1954 and continued during 1955, and treatment of the breeding rivers was begun early in 1956. The present paper describes the pre-treatment observations and the post-treatment results for the first three years of the scheme.

Description of the Area.

The area chosen for the control project (map 1) comprised some 1,200 square miles of northern Abuja Emirate between 8°55′ and 9°20′ N. and 6°50′ and 7°30′ E. It is an area of hilly or undulating country lying on pre-Cambrian granite which

gives rise to rocky-bedded rivers with rapids and falls. The area is drained principally by three main rivers, the Iku, Tapa and Usuman, which flow in a south-westerly direction to join the large Gurara river, which itself rises on the western fringe of the Jos Plateau and joins the Niger about 60 miles south of the control area.



Map 1.—The area of the Abuja control project for *S. damnosum*, showing the pre-treatment breeding sites, treatment points, and the motorable tracks constructed.

In addition to the main rivers, the area is drained by a multiplicity of seasonal streams which, like the main rivers, generally have bands of fringing forest along their banks. The vegetation where the land is not farmed is principally secondary Guinea Savannah, but there are numerous small patches of dense forest. The oil palm, *Elaeis guineensis*, is a characteristic feature of the area, both along the rivers and on the recently farmed areas.

The altitude over most of the project area is from 1,000–1,800 ft. above sea-level, but is only some 600 ft. in the south-west and reaches 2,500 ft. in the north-east. The dry season (months with under one inch rainfall) is short and lasts only from November to February, the rains being correspondingly lengthy; the rainfall is very high for Northern Nigeria and averages 65 in. per annum in Abuja township, the Emirate headquarters and a small native town of 4,000 people. The inhabitants of Abuja town and a small area around it are Mohammedan Hausas, but in the remainder of the area they are almost entirely a pagan population belonging to the Gwari tribe; the population density in the area is 26 persons per sq. mile, which is low in comparison wth most parts of the country. Onchocerciasis is endemic, and all villages in the area are infected.

Pre-treatment Observations on *S. damnosum.*

Before any control of *S. damnosum* could be attempted it was necessary to establish which stretches of river in the area formed the breeding grounds, for when the area of Abuja was selected for the control project it was only known in a general way that *S. damnosum* occurred, and no detailed knowledge was available on the extent of the breeding sites. Information was also required on the incidence of the adult fly before any application of larvicide to the breeding grounds took place, since it was intended that the principal criterion of successful control should be a reduction in the adult fly population after insecticidal treatment of the rivers.

Surveys were made for the immature stages of *S. damnosum* in the watercourses of the area, and for the incidence of the adult fly, between September 1954 and December 1955.

Surveys for the breeding grounds.

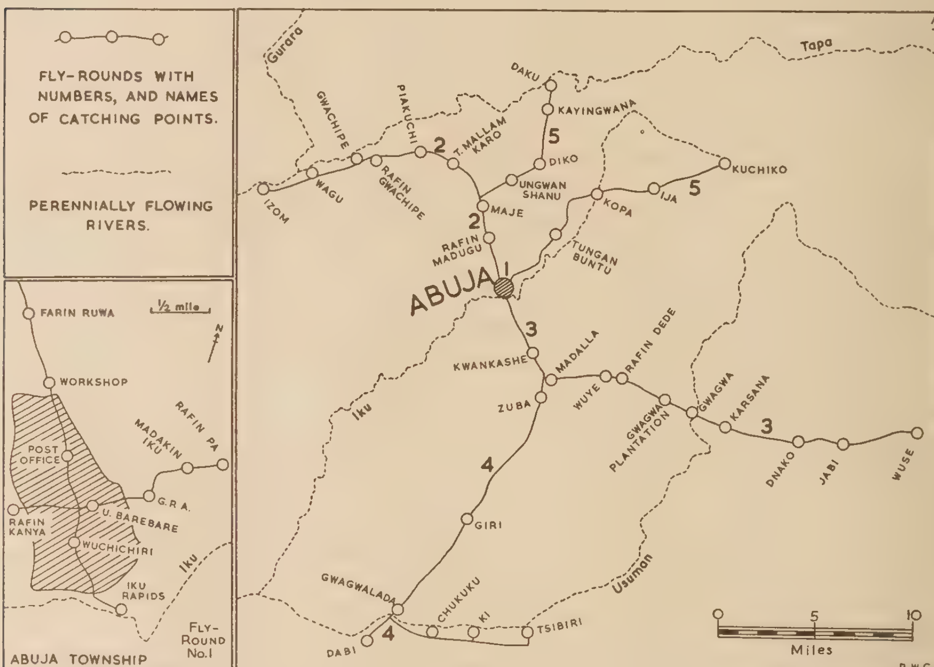
Larvae and pupae of all species of *Simulium* were collected from the rivers and streams of the area in both wet and dry seasons and the sites at which immature stages of *S. damnosum* were collected were mapped. The breeding distribution was determined in this way, and it soon became apparent that breeding of *S. damnosum* was confined to the fast-flowing rocky stretches of the large perennial rivers, and that no breeding occurred in the side streams except for the very occasional pupa found in these small tributaries at the height of the rains. Breeding therefore occurred almost entirely along the Iku, Tapa, Usuman and Gurara rivers; the pre-treatment breeding sites are shown on map 1. Breeding was by no means continuous along these main rivers, for there were breaks in the breeding grounds where the rivers ran in slow-flowing muddy stretches, and much of the upper reaches of the rivers (*e.g.*, the Iku above Abuja and the Tapa upstream of Chauma) were unsuited to breeding. But breeding occurred fairly generally along some 18 miles of the Iku river, 22 miles of the Tapa river from its confluence with the Gurara, and along about 70 miles of the Usuman river. In addition to these, most of the Gurara river formed a breeding ground.

Surveys for the adult fly.

Catches of adults were made throughout the area by means of fly-rounds, which consisted of series of catching points arranged in a particular sequence and visited at regular intervals. A total of 43 catching points was selected in the area and the points were arranged into five fly-rounds, which radiated from Abuja town and included one fly-round in the township itself. The fly-rounds are shown on map 2. The fly-rounds extended for 13 miles to the west of Abuja, 21 to the east, 10 miles to the north and 18 miles to the south. Difficulties of terrain and lack of tracks made it necessary to site most of the catching points on roads or sufficiently near them so that no time should be wasted in long walks to the catching points, and to enable catches to be made each day at a considerable distance from the base at Abuja. Almost all fly-rounds were carried out by Land-Rover, but transport difficulties sometimes made it necessary to use bicycles. Consequently, it was not always possible to carry out the fly-catch at exactly the same time at any one point on different days, especially as road and weather conditions often made it impossible to reach a particular point at a given time. But, so far as possible, each fly-round was carried out on a particular day and the catching points were visited in the same order, so as to make the conditions of collection as similar as possible each time the fly-round was carried out.

When working the fly-rounds each catching point was visited for a period of 15 minutes during which fly-boys collected all flies settling on them (for practical purposes, settling rate in *S. damnosum* is equivalent to biting rate) when their legs were exposed for the attraction of flies. The flies were collected individually

in specimen tubes, and the numbers counted and recorded at the end of each period, together with the name of the catching point, and the number of fly-boys employed (this was normally three, but circumstances such as illness sometimes reduced the number). At the end of each month the number of flies collected at each catching point was totalled, and the density at that point expressed as the number of flies per observation period (one catcher for 15 minutes), or as the



Map 2.—The fly-rounds and catching points, in the project area, used in assessing adult density of *S. damnosum*.

number of flies per boy-hour (F.B.H.). Density expressed in this way overcame the difficulty of different numbers of fly-boys being employed at different times, but the number of fly-boys engaged was kept constant whenever possible.

The fly-rounds showed that, before treatment, adults of *S. damnosum* were widespread in the area during the rains, and that they could be collected almost anywhere within five miles of the breeding rivers, but that beyond this distance they became scarce. Very different densities were, however, found to exist at different catching points. The results of the pre-treatment surveys are summarised later in comparison with the post-treatment results.

Selection of River-treatment Points and Season for Application of Larvicide.

The preliminary breeding surveys indicated where it would be necessary to apply the insecticide if control was to be successful, and mapping of the breeding grounds enabled the treatment points to be selected. A recently published World Health Organisation report (1954) had stated that DDT (the insecticide which was to be used in the control project) at 0·5 parts per million p,p′ isomer in river water should achieve sterilisation for about 40 miles if delivered over a period of

30 minutes. It was therefore decided to have a single treatment point each on the Iku and Tapa rivers, where the infested stretch was under 40 miles in length, and two treatment points on the Usuman river which was infested for about 70 miles.

It was decided not to attempt control on the Gurara river, where it was impossible to get above the highest breeding grounds, and because of its size and general inaccessibility. It was realised that reinfestation of the treated rivers must inevitably occur from the untreated Gurara, but it was one of the objectives of the scheme to ascertain the rate at which such reinfestation might be expected to occur. It was not expected that eradication would be achieved in the area, since other infested rivers in Niger, Zaria and Benue Provinces (*e.g.*, the rivers Chanchaga, Bobo, Dinya and Uke) lie within 20 or 30 miles of the area.

For the applications of larvicide in 1956, four treatment points were selected (see map 1), *viz.*, on the Iku river at Abuja (point 1), on the Tapa river near the village of Chauma (point 2), and on the Usuman river at the village of Mahapa (point 3) and at Gwagwa (point 4) where a bridge crosses the river carrying the Abuja-Keffi road. From the experience gained as a result of the 1956 treatment it was found necessary to establish the following three additional treatment points in 1957, an extra one on the Tapa river at Tapa Falls (point 5) and two extra ones on the Usuman at Kwango village (point 6) and at Gwagwalada (point 7). It would have been desirable to have a second treatment point on the Iku river, downstream from Abuja, for the 1957 treatment, but the extreme inaccessibility of this stretch made it impracticable to establish a point on the lower Iku anywhere between Abuja town and the Iku-Usuman confluence.

Both the 1956 and 1957 treatments were carried out in the late dry season and very early rains, for at this time the rivers are at their lowest level and consequently the quantities of insecticide required are very much less than they would be if control were attempted in the rains. In the dry season also, larvae and pupae are confined to a much less extensive breeding area than in the wet season when much more of the river beds and vegetation is submerged, while if treatment is carried out in the dry season in the perennially flowing rivers there is no chance of overlooking possible breeding sites in the seasonally flowing tributaries as these are dry or stagnant from about January to June. Practical considerations also determined that treatment should be done in the dry season, for in the absence of bridges over the rivers it was necessary for the larvicide dispensers to be supported over the rivers by labourers standing in the water, which could only be done when the rivers were at a level low enough to permit wading; furthermore the temporary, dry-season motor tracks referred to below would not be serviceable during the rains and it was essential that once treatment had commenced it should continue without interruption due to bad weather and road conditions. In this connection it is worth noting that the late dry season was also chosen for the French larvicide campaign against *S. damnosum* on the Kebbi river, Chad Territory (Taufflieb, 1955, 1956).

Construction of dry-season motorable tracks.

Two of the four original treatment points selected in 1956 were over five miles from the nearest motorable tracks, and it became necessary to open motorable routes so that materials and labour could be transported to the treatment points without difficulty, as application of insecticide to the rivers was not thought feasible unless the treatment points could be reached by road. Local labour was engaged through the co-operation of the Abuja Native Administration and motorable tracks were constructed in January 1956 from Diko village to the Tapa river at Chauma and from Maitama village to the Usuman river at Mahapa. The former of these roads was very easily opened, but the latter was difficult as it had to traverse a 500-ft.-high escarpment and cross several streams.

The addition of the three extra treatment points for the 1957 campaign necessitated the construction of a further three miles of track from Kuje village to the Usuman, and the re-opening of an old track from Maje village to the Tapa, while it was also necessary to reopen the tracks which had been constructed for the 1956 treatment as they had been badly washed away during the intervening wet season. The positions of the tracks constructed are shown on map 1.

Insecticide Used and Methods of Application.

Insecticide and dosage employed.

DDT was chosen since this insecticide had already proved itself effective as a larvicide against *Simulium* spp. in several parts of the world, including Alaska (Gjullin, Cope & others, 1949; Gjullin, Cross & Applewhite, 1950; Gjullin, Sleeper & Husman, 1949; Travis & others, 1951), Canada (Arnason & others, 1949; Hocking, 1950, 1953; Hocking & Richards, 1952; Hocking, Twinn & McDuffie, 1949; Twinn, 1950), Ghana (Noel-Buxton, 1956), Guatemala (Fairchild & Barreda, 1945; Lea & Dalmat, 1954, 1955*a*, 1955*b*), Kenya (Garnham & McMahon, 1947), Uganda (Barnley, 1953) and United States of America (Goulding & Deonier, 1950; Jamnback & Collins, 1955; Kindler & Regan, 1949).

A technical grade of DDT containing 70 per cent. p,p′ isomer was used, and was run into the rivers in diesel oil for a period of 30 minutes at each treatment.

A different technique for estimation of dosage rate was employed in the two years. In 1956, the same weight of DDT was used at all applications and for all three rivers and, since the flow in different rivers and at different times was not always the same, the dosage rate varied between one application and another, and between one river and another; but it was calculated from a knowledge of the usual dry-season volume of the rivers that the constant quantity of DDT (28 lb. technical, containing 19·6 lb. p,p′ isomer) used would give a dosage between 1 and 2 parts per million of p,p′ DDT in the river water, unless early rains or exceptional drought raised or lowered the rivers so that the dosage rate was correspondingly lowered or raised. Calculation showed that 19·6 lb. of p,p′ DDT applied over 30 minutes would produce a dosage rate between 2 and 1 p.p.m. in rivers flowing at between 88 and 175 cu. ft. per second. It was thought unlikely that flows outside these limits would be very frequent, and, in fact, they occurred only seven times out of the 48 applications made in 1956, when local rain-storms raised the rivers and diluted the dosage to below 1 p.p.m. The river discharge was measured (see below) at the time of each application, and from this, the dosage rate was calculated. The highest and lowest dosage rates per application were 2 and 0·3 p.p.m. The use of a constant quantity of DDT at each application irrespective of the flow of the river would be a very inexact procedure in the wet season, when rapid fluctuations occur in the volume of flow, but would seem to be a practical approach in the dry season when there is very little day-to-day variation in flow. Subsequent calculations showed that the mean dosage applied in 1956 was 1·4 p.p.m. of p,p′ DDT (S.D. = 0·5 p.p.m.).

In 1957, the quantity of DDT used was varied at each application according to the flow of the river at the time, so as to produce a constant dosage of 1 p.p.m.

Estimation of river flow.

River discharge was measured in cusecs (cubic feet per second) for each application; this was required to calculate the dosage applied in 1956 or for estimating, in 1957, the quantity of DDT required to produce the desired dosage of 1 p.p.m. Flow was assessed for each application as near as possible to the downstream point that, it was hoped, the insecticide would reach, and not at the treatment point itself, and the measuring points were situated where the character of the river was reasonably uniform. The depth, for purposes of flow calculation,

was taken as the mean of five measurements made at right angles to the direction of flow, and the width was measured with a graduated rope. Speed of flow was ascertained by means of a Watts current meter, and the river discharge was calculated in cusecs as the product of the three measurements.

Calculation of the weight of DDT required.

For the 1957 treatment, the weight of DDT required for each application was calculated in the manner recommended by the World Health Organisation (1954), and the method is described briefly below:—

The application time was 30 minutes. A cubic foot of water weighs 62 lb., and a flow of one cusec for 30 minutes therefore discharges 62 × 60 × 30 lb. of water (= 111,600 lb.). Hence, to produce a dosage rate of one part per million of DDT in the water flowing at one cusec over a period of 30 minutes, 0·1116 lb. DDT is required. But the DDT employed contained only 70 per cent. toxic isomer so that 0·1116 × 100/70 lb. (= 0·16 lb.) of DDT, technical grade, was needed to produce 1 p.p.m. p,p′ DDT in a flow of *one* cusec for 30 minutes.

As a flow of one cusec for the application time of 30 minutes required 0·16 lb. of DDT, technical grade, the weight required on each occasion was readily calculated as: flow in cusecs × 0·16 lb., *e.g.*, a river flowing at 132 cu. ft. per second required 132 × 0·16 lb. (= 21 lb. 2 oz.) of technical DDT applied over 30 minutes for a dosage rate of 1 p.p.m.

Frequency of application and duration of treatment.

The river at each treatment point received one application per week for a total period of 12 weeks. There were four treatment points and hence 48 applications in 1956, and seven treatment points with a total of 84 applications in 1957. Each point application was made on the same day each week so there was a regular interval of seven days between applications at any one point.

In selecting the frequency of application, Barnley's (1953) estimate of 6–8 days as the length of larval life in *S. damnosum* was accepted since no definite evidence was available on the larval life in the project area; but it was thought that larval life was longer than the five days recorded by Wanson (1950) in the Belgian Congo, although it may be noted that it is almost certainly shorter than the 10–13 days recently recorded by Crisp (1956) in Ghana.

It was assumed that the DDT would not be toxic to pupae of *Simulium* since it had been found elsewhere (Hocking, 1950; Hocking, Twinn & McDuffie, 1949) that the pupal stage was almost unaffected by insecticides, although more recently Taufflieb (1955) considered that pupae of *S. damnosum* were killed by applications of lindane (γ BHC) in the Mayo Kebbi control scheme, French Chad Territory.

Methods of preparing insecticide and dosing the rivers.

The DDT was applied to the rivers in diesel oil. Technical DDT is insoluble in water but it was found that diesel oil was a satisfactory carrier and spreader of the insecticide. During application, the oil could be seen fanning out across the river just below the application point and getting well stirred in the turbulent places in which *S. damnosum* principally bred.

The DDT, equipment, staff and labourers were taken to each treatment point by Land-Rover; the drums of diesel oil were dumped and left at the treatment points before applications were due to commence, so as to avoid daily transport of this item. At each application, the oil was measured out first into containers preparatory to receiving the DDT; a total of 22 gals. (half drum) of diesel oil was used at each application as it was found that this quantity would be delivered from the dispensing cans in 30 minutes. It should be noted that one of the objects of the oil was to provide the bulk necessary to ensure the delivery of the DDT over the comparatively prolonged period of half an hour.

The 22 gals. of oil were divided equally (3·66 gals. per container) into six kerosene tins (5 U.S. gals. capacity), each being marked internally with a painted ring indicating the correct measure. Three of these tins were the dispensing tins from which the larvicide would be delivered into the river, and the other three served as containers from which the dispensing tins would be replenished after 15 minutes.

After measuring out the diesel oil into the tins the requisite quantity of DDT (see p. 720) was weighed out and divided equally into six shallow metal pans with handles (head-pans); these head-pans were then warmed over fires made in shallow pits in the ground until the DDT was just molten. During the heating, the DDT was stirred and the lumps broken, and care was taken to see that it did not become over-heated with consequent loss from vaporisation. When the DDT was just liquid the contents of each head-pan was poured into the diesel oil in one of the tins and the mixture agitated for a few minutes. The object of warming was to hasten the rather slow solvent action of diesel oil on the DDT, and it was found that the DDT did not crystallise out for several hours.

The three dispensing tins each had a single central hole in the bottom of such a size (diameter of a 3-in. nail) that the 3·66 gals. would run through in 15 minutes; the holes were closed with wooden plugs which could be withdrawn by a cord when application began. The dispensing tins were also provided with rope handles so that they could be slung on poles supported between labourers. Since each dispensing tin would deliver its contents in 15 minutes, it would then be replenished with the same amount of larvicide for a further run-through of 15 minutes; in this way the desired application time of 30 minutes would be obtained.

When all six tins were ready they were taken down to the river from the mixing point (which was as near as possible to the water's edge); the dispensing tins were supported on poles held between the shoulders of pairs of labourers, and the replenishing tins were stood nearby, ready to refill the dispensers when these were empty after 15 minutes. The three pairs of labourers, each pair supporting a dispensing tin, stood in the river at suitable intervals across its breadth, and when all were in position the plugs were withdrawn from the dispensers and application began; the labourers remained in the river, supporting the tins, for the 30 minutes' application. The application time was measured with a stop-watch; the time was found to vary slightly between about 28 and 31 minutes, and was occasionally slightly longer when an impurity in the DDT, or a piece of fallen twig or the like, from the fringing vegetation, caused a momentary blocking of a dispensing hole; but this only occurred infrequently since the labourers kept the contents of the tins slowly stirred during application, and the mean application time was 30·4 minutes.

Possible blocking of the orifices in the dispensing tins was one of the reasons why these were not suspended across the rivers on ropes as recommended by the World Health Organisation (1954); some of the rivers being treated were over 100 ft. across, and, on the banks, suitable trees for attachment of ropes were not always present, whilst the weight to be suspended would have been quite considerable, so that the WHO recommendation was considered in this respect quite impractical. But in both 1956 and 1957 the rivers remained sufficiently low to be entered by the labourers with the dispensers, although once or twice, after freak storms, the men had to stand in water reaching to the thighs. In general, this method of suspending the dispensers between men standing in pairs would seem to be very satisfactory for *dry season* applications.

Before any application of larvicide had been attempted, considerable attention had been paid to the type of apparatus to be used for dispensing the larvicide into the rivers, since the simple perforated tin (such as had been used by Garnham & McMahon, 1947, and recommended in the WHO report, 1954) would deliver the

insecticide at an uneven rate with a high dosage rate at the beginning of the application and a low one at the end. The type of apparatus described by Hocking (1950), which delivers an even flow, was preferable on scientific grounds but it was found that it could not be constructed in Nigeria, whilst it was thought that any too elaborate or delicate apparatus would certainly not survive for long on the rough tracks over which it would have to be carried, or in the hands of the untutored African assistant. It was therefore decided to resort to the simple perforated delivery tin, which in spite of the objections to it on theoretical grounds, proved easy in use to the native labourer. It should be mentioned here that although the treatment technique was aimed at being as reliable and accurate as possible, it had at the same time to be made as simple as possible so that it could be operated as a routine by unskilled Africans. But although they were the operatives, every application was personally supervised by an entomologist.

Treatment periods.

The first year's treatment period was from 5th March until 24th May 1956, and the second year's from 4th February to 26th April 1957. Rainfall affected the levels of the rivers on a few days towards the end of the first year's period, and as a consequence of this it was planned to carry out the 1957 treatment earlier in the year.

By the middle of the dry season of 1956–57 it was apparent that the rivers would reach a very low level, but since it was impossible to tell when the wet season would begin it was decided to commence the 1957 treatment in February as planned.

It was unfortunate that the second year's treatment coincided with this exceptional drought period in which the rivers reached an unprecedentedly low level and almost ceased to flow; according to the local native people it was the severest dry season for about 40 years since the Wuchichiri stream in Abuja town (by which they assess the severity of the dry season and which normally survives the dry season as a series of large stagnant pools) had completely dried out. During the second year's treatment, only small traces of rain fell, and these had no discernible effect on the rivers as they were rapidly absorbed by the parched ground.

In view of the abnormal condition of the rivers, the 1956 technique of a constant weight of DDT at each application was abandoned in favour of calculating the exact quantity required for each application to produce a fixed dosage of 1 p.p.m. (see p. 721). It was thought that, because of the low state of the rivers, the fixed-quantity technique might produce very considerable over-dosing, with possible mortality amongst fish (some mortality had occurred during the 1956 treatment—see below).

Post-treatment breeding surveys and results.

The effect of treatment on the immature stages of *S. damnosum* was assessed by surveys for the larval and pupal stages; these were carried out during the treatment period and subsequently until the end of June. The flooded condition of the rivers in the rains, from July to October, made it impossible to continue surveys during this period because the possible breeding sites were inaccessible, but surveys were resumed in November with the return of the dry season and were continued until the end of December.

The surveys were made principally on the Tapa and Usuman rivers which were accessible at several points at different distances below the treatment points; some surveys were also made on the Iku river for five miles below the treatment point at Abuja, but the nature of the country made it impracticable to attempt surveys at a greater distance downstream on this river.

Effects of Treatment on Immature Stages.

The 1956 treatment.

On the Tapa river, larvae and pupae were still present after the sixth week of treatment at a point (Laiba) nine miles below the treatment point, and were apparently unaffected at further distances downstream; after the ninth application no larvae remained at Laiba or at a point (Tapa Falls) 13 miles downstream from the treatment point, but breeding continued (though there were fewer larvae and pupae) at Gwachipe and Wagu (23 and 26 miles below the treatment point). After the eleventh application, no further breeding was found at Gwachipe, but breeding continued at Wagu, and surveys after the twelfth application (end of the treatment period) showed that no larvae and pupae could be found anywhere between the treatment point (Chauma) and Gwachipe, but that larvae and pupae were still present at Wagu. The treatment therefore appeared to be effective on the Tapa river for a distance of some 23 miles. Similar surveys on the Usuman river showed no larvae and pupae for 22 miles below the Mahapa treatment point, but some larvae were still present at Tsibiri, 15 miles below the Gwagwa treatment point, after the twelve weeks' period of treatment had been completed. After completion of the treatment, no larvae or pupae could be found in the Iku river for five miles below Abuja, but as already mentioned, no surveys could be made below this point.

It was tentatively concluded from the post-treatment surveys of the immature stages in 1956 that the treatment with DDT had been effective in eliminating larvae for an approximate distance of 15–23 miles below the treatment points, but that it had certainly not been fully effective further than this. No effect on breeding was noticed in the Gurara river below the confluence with the Tapa.

The surveys, resumed after the rains, showed that larvae and pupae were again present in the stretches of river which had been cleared earlier, although their numbers were apparently fewer than usual (*i.e.*, before treatment). This finding was very remarkable in view of the extremely low densities of adult flies which had existed during the intervening wet season (see succeeding section), for re-infestation of the cleared breeding grounds had evidently been brought about by a very low adult population and for a maximum distance of 23 miles upstream from the nearest untreated breeding site.

The 1957 treatment.

The results after the 1957 treatment were less satisfactory than in the previous year, and the probable reasons for this are discussed later. After the treatment period, larvae were still present at points eight miles below the Gwagwalada and Chauma treatment points, but none could be found for the 22 miles below the Mahapa point (*i.e.*, as far as the Gwagwa point), for 13 miles below the Tapa Falls point, 11 miles below the Gwagwa point (*i.e.*, to the Kwango point), and nine miles below the Kwango point. But, in view of the 1957 findings on the adult density (see below), it seems likely that some breeding continued unobserved in unsurveyed stretches along the rivers (it being clearly impossible, when dealing with over 100 miles of breeding or potential breeding ground, to see every part of the rivers).

After the wet season of 1957, breeding was again re-established in all the cleared stretches of river as it had been after the 1956 rains.

Effects of Treatment on Fly Density.

No satisfactory means has as yet been devised for assessing the population density of the immature stages of Simuliids, so that reductions in larval density as a result of insecticidal treatment cannot at present be measured with any precision. But the number of flies settling to bite human bait per boy-hour

(F.B.H.) has been found to be a reasonably suitable, though no doubt imperfect, means of estimating the density of adult flies, at least in the case of *S. damnosum*. It was therefore thought that the success of the control measures could best be assessed by a comparison of the pre- and post-treatment adult fly densities. The methods used in collecting data on the numbers of the adult fly have been described in an earlier section (p. 717).

In Northern Nigeria, adults of *S. damnosum* are abundant in the wet season from about May or June until November, and very scarce (or at least difficult to locate) in the dry season from December to April; this applies even in areas where there is continuous breeding throughout the year in perennially flowing rivers. As the fly density is normally very low in the dry-season months it was thought that the discovery of a very low or *nil* density in these months, following the application of control measures, would not necessarily indicate that the treatment had been successful. It was therefore decided to restrict the observations on the adult density principally to the wet-season months in which a reduction in density after treatment would be more likely to be readily apparent, and observations were accordingly made from June to December each year. This was convenient also from the practical point of view since in the remainder of the year, January to May, staff were busily engaged with such preparations

TABLE I.

The monthly pre-treatment and post-treatment densities of *S. damnosum* in the project area and in Abuja township.

Year	Month	Project area			Abuja township		
		Flies collected	Boy-hours	Density (F.B.H.)	Flies collected	Boy-hours	Density (F.B.H.)
1955 Before larvicidal control	June ..	139	42·25	3·29	78	25·00	3·12
	July ..	300	36·25	8·28	169	13·75	12·29
	August	830	52·00	15·96	327	25·25	12·95
	September	624	37·25	16·75	445	16·50	27·00
	October	211	24·75	8·53	110	10·25	10·73
	November	112	38·75	2·89	59	19·00	3·11
	December	25	21·00	1·19	1	10·25	0·10
Totals		2241	252·25		1189	120·00	
1956 After larvicidal control	June ..	8	81·25	0·10	3	44·25	0·07
	July ..	18	86·00	0·21	4	39·50	0·10
	August	32	100·50	0·32	0	48·50	0·00
	September	18	131·75	0·14	6	72·50	0·08
	October	125	134·50	0·93	52	67·50	0·77
	November	11	70·00	0·16	5	30·00	0·17
	December	4	63·00	0·06	1	30·00	0·03
Totals		216	667·00		71	332·25	
1957 After larvicidal control	June ..	38	89·50	0·42	20	40·00	0·50
	July ..	362	175·25	2·07	109	73·00	1·49
	August	571	194·75	2·93	251	99·25	2·53
	September	452	213·50	2·12	263	100·00	2·63
	October	277	226·25	1·22	192	109·25	1·76
	November	284	262·75	1·08	131	123·75	1·06
	December	49	201·50	0·24	12	95·00	0·13
Totals		2033	1363·50		978	640·25	

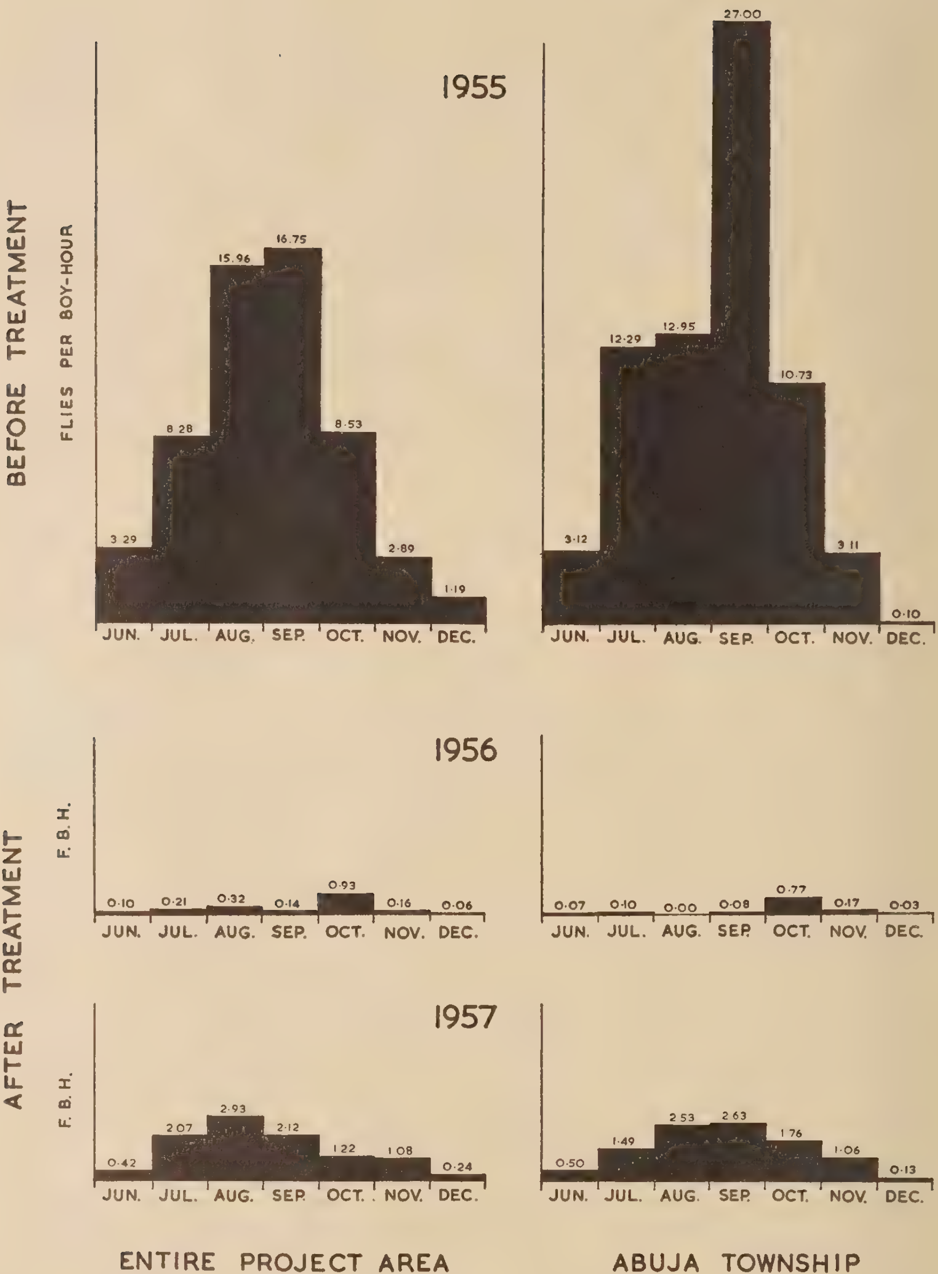


Fig. 1.—The adult density of *Simulium damnosum*, expressed as flies caught per boy-hour, in the months June to December in three successive years, one before and two after treatment of the breeding grounds with larvicide.

for the campaign as construction of tracks, with the treatment programme, and with post-treatment breeding surveys.

The data on adults for the months June to December in each year are summarised in Table I. The data given are those obtained from the fly-rounds shown on map 2. Detailed data for each of the 43 catching points is shown in the Appendix to this paper. Summarised data for both the project area as a whole and for Abuja township, which lies near the centre of the area, are shown in Table I. It was thought that if similar fluctuations in density occurred from month to month in both the township and the whole area it would serve to confirm whether it was legitimate to aggregate the results from individual catching points into a project-area total and to consider the whole area as a single unit. Inspection of Table I and fig. 1 shows that very similar fluctuations in density did in fact occur in Abuja and the whole area. It would have been desirable to establish an observation site well outside the project area, so as to assess the normal density prevailing during the same periods in an area which had not received insecticidal treatment; but many practical difficulties prevented this.

The results are also shown in histogram form in fig. 1. It will be seen that after the treatment in 1956 the fly density did not reach as high as 1 F.B.H. in any month in either the whole project area or in Abuja town, although in October 1956 the density was somewhat higher than in the other months, possibly because by this time (the end of the rains) some reinfestation of the cleared breeding grounds, from the uncleared stretches farther downstream had occurred, or there had been some influx of flies from the treated periphery of the project area. By November, when it was possible to enter the rivers again for breeding surveys, it was found that reinfestation of the cleared stretches of river had occurred (see p. 724) in spite of the exceedingly low density of adult flies found to exist during the wet season. But it is probable that reinfestation along a river from an untreated breeding site would be much more rapid than reinfestation across country from a separate river. The rise in October occurred in Abuja township as well as the whole project area although in August in the township no flies had been caught in 48·5 boy-hours. It will be seen that the rise in density in October 1956 was short-lived and that density had dropped again to a very low level in November and lower still in December once the dry season had returned.

In 1957, the results were less encouraging. Although the fly density was very considerably lower than that existing in 1955 before treatment, it was a great deal higher than in 1956; but it is certain that the control in the breeding grounds had not been nearly as complete in 1957 as it had been in the previous year, and there is little doubt that higher numbers of flies in the rains of 1957 were the result of inadequate control of the larvae. This is further discussed below.

Nevertheless there seems no doubt that the very striking difference between the pre- and post-treatment densities of adult flies is attributable to the control of larvae in the breeding sites, since it is very unlikely that year-to-year differences in density of this magnitude would occur in nature and since a large measure of control was shown, by means of the breeding surveys, to have been achieved against the immature stages.

It is considered that in the first year of treatment a very high degree of control was achieved; in the pre-treatment year, 1955, a total of 2,241 flies was collected between June and December in 252·25 boy-hours (see Table I), giving a mean density of 8·88 F.B.H. After treatment in 1956, a total of 216 flies was collected in 667·00 boy-hours over the same period, a mean density of 0·32 F.B.H. Hence the post-treatment density in 1956 was only 3·60 per cent. of that existing before treatment, so that, assuming that had there been no treatment, the 1956 density would have been similar to that in 1955, the first year's

campaign brought about a reduction in the adult fly population of 96·40 per cent. Between June and December 1957 a total of 2,033 flies was collected in the project area in 1,363·5 boy-hours, giving a mean density of 1·49 F.B.H., or 16·78 per cent. of the 1955 pre-treatment density. Hence there was an approximate reduction in density in 1957 of 83·22 per cent. as compared with the pre-treatment density and as compared with a reduction of 96·40 per cent. in 1956.

Effect of Treatment on other Organisms.

Similar effects to those of *S. damnosum* were found to occur with the immature stages of other species of *Simulium*. The treated rivers were breeding places of *S. bovis* De Meillon, *S. cervicornutum* Pomeroy, *S. adersi* Pomeroy and *S. medusaeforme* form *hargreavesi* Gibbins, and the larvae and pupae of these species were eliminated for about the same distances as those of *S. damnosum*. By the dry season following treatment, all except *S. bovis* appeared to be completely re-established in their former breeding sites, but re-establishment of the latter species seemed to be slower in that only a few pupae were found in sites only a short distance upstream from the unaffected breeding grounds.

No effect from the DDT was observed on other insect life such as larval and adult Coleoptera (*e.g.*, Gyrinidae), larval Trichoptera, aquatic Hemiptera, the nymphs of Ephemeroptera or Odonata, or on Crustacea and tadpoles. But some mortality, presumed to be due to the DDT, was observed among fish fry during the treatment periods; the largest fish found dead (24 hours after an application of DDT to the river) measured five inches in length and was identified as of a species of *Tilapia*, but apparently no fully grown fish were killed. There were no traces of diesel oil on the dead fish, and it is possible that they had been killed by an abnormally high concentration of DDT, since all the dead fish were collected from places where eddies or rock hollows caused a temporary build-up of larvicide; such places were found to be numerous along the rivers where the configuration of the bed caused the water to collect in large pools with only one or two narrow channels for the gradual egress of the water. Hold-ups to the flow of larvicide were also caused by fallen trees, and by the construction of fish traps by the native populace, and a few small dead fish were found among these obstacles also. No evidence was found that the DDT caused any mortality among fish in normal circumstances where the rivers were flowing uninterruptedly.

TABLE II.

The cost of the Abuja experiment for control of *Simulium* during the period January 1956–December 1957.

	1956	*1957*
Application of larvicide		
Labour : road construction	£421	£154
Labour : for application	£45	£39
Diesel oil (at 2s. 10d. per gallon)	£153	£268
Technical DDT (at £324 per ton)	£193	£305
Rail freight on DDT	£8	£14
Transport of materials	£33	£38
Running and maintenance of Land-Rover	£70	£94
	£923	£912
Post-treatment fly-rounds and breeding surveys		
Running and maintenance of Land-Rover	£123	£138
Total expenditure	£1046	£1050

The Cost of the Control Project.

By far the major part of the expenditure for the project was concerned with the programmes directly or indirectly related to the applications of the larvicide. The follow-up observations required very little over and above normal recurrent expenditure on staff. The expenditure on the project for 1956–57, exclusive of personal emoluments and allowances of departmental staff, is summarised briefly in Table II. The West African pound is at par with sterling.

The construction of the motorable tracks for reaching the treatment points cost a little under £39 per mile in 1956. The roads were constructed during the author's absence on leave, at a time when it was not possible for reliable supervision to be given, and it is likely that the tracks could have been made for somewhat less than this, as it was found in 1957 that a mile of new track could be opened in ordinary country for about £12–£15. In more difficult country it would have cost about £20–£25 per mile at the labour wage of 2/1d. per day obtaining in the Abuja area at the time. Re-opening of pre-existing tracks was found to cost £8 per mile, or about two-thirds of the cost of new track; the cost of re-opening old tracks was comparatively high because of the reconstruction of the temporary dry-season bridges that had been washed away in the rains.

Tools for construction of tracks, picks, shovels, head-pans, axes, and matchets, were obtained from Medical Department stores, and no capital expenditure was incurred on this item, or on scales, ropes and other equipment used in application of the larvicide. The Watts current meter used for measurements of river discharge was bought for use in *Simulium* control and together with accessories cost £141.

Discussion.

In 1956, the mean dosage rate per application, was 1·4 p.p.m. p,p'DDT (S.D. = 0·5 p.p.m.), and was effective in eliminating breeding of *S. damnosum* for 15–23 miles below the treatment points, but, at greater distances than these, breeding was only reduced. Six months after the end of the treatment period it was found that breeding was re-established on a moderate scale in all the cleared stretches of river in spite of the very low adult density, averaging only 0·35 F.B.H., during this period from June to November, this density representing only 3·65 per cent. (*i.e.*, a reduction of 96·35%) of that in the same period of the year prior to treatment.

It seems likely that reinfestation of the breeding grounds occurred by movement of flies upstream from the uncleared breeding sites below the cleared stretches, rather than across country from other rivers, since examination of the data from individual catching points (see Appendix, p. 735) shows that higher catches were generally recorded, after treatment, at points near the rivers, whereas, before treatment, catches were often higher away from the rivers than close to them. It appears therefore that, *along* rivers at any rate, reinfestation of breeding sites can occur very rapidly and be brought about by very low adult fly densities.

As a result of the 1956 findings, it was decided, in order to obtain a greater degree of control, to increase the number of treatment points from four to seven in 1957, and it was thought that additional treatment points downstream from those used in 1956 would serve to deal with sites where breeding had not been fully controlled earlier. In this way it was hoped that all breeding would be eliminated from the Iku, Tapa and Usuman rivers until such time as reinfestation from the Gurara occurred. But the results obtained in 1957 were disappointing, and control was less satisfactory than in the previous year in spite of the extra treatment points. The reason for this is undoubtedly that in 1957 the treatment was carried out in an exceptionally severe dry season when the rivers

reached such a low level that they were often little more than trickles. Observations showed that the larvicide was frequently held up by various obstacles, so that although the river was treated at a rate of 1 p.p.m. DDT, this concentration almost certainly did not reach most of the breeding sites, and probably many sites several miles downstream from the treatment points escaped treatment altogether. The principal obstruction to the passage of the larvicide was provided by dams of earth, boulders and tree trunks made by local native fishermen as fish traps or to divert the water to suitable fishing pools. These dams were very numerous on suitable parts of the rivers and were often quite elaborate stone structures through which the water could percolate only slowly from the bottom. Thus the effect of the dams was to impede the flow of larvicide very drastically, since the diesel oil conveying the DDT largely floated upon the broad pools created above the dams and only gradually seeped away downstream. In addition to the fishermen's dams, the larvicide was also frequently held up by natural obstacles in the rock formation of the river bed, such as rock hollows which created eddies that revolved the larvicide with only gradual dispersion down the river, or by tree roots and fallen trees, while some was also lost by being washed into semi-stagnant pools along the river margins. Although it was realised that the larvicide was being held up, almost nothing could be done to assist its free passage downstream because of the impossibility of reaching every point along more than 100 miles of river, especially as the nature of the terrain made much of the river courses very inaccessible.

Failure of the DDT adequately to reach and control larvae in their breeding sites during 1957 is almost certainly the reason for the higher adult fly catches in that year than in 1956 (see fig. 1). There appears to be no need to fear a more sinister explanation such as the possibility of development of resistance. Notwithstanding the obstacles to the larvicide, some control was undoubtedly achieved, since breeding was eliminated for at least 8–9 miles below the treatment points and in some cases for further distances where there was little human population and therefore fishing dams were fewer. The adult fly density between June and November 1957 averaged 1·71 F.B.H. in the whole project area, or 17·85 per cent. (*i.e.*, a reduction of 82·15%) of the density recorded in the same period of the pre-treatment year 1955; but the density in 1957 was about five times greater than in 1956 when the density between June and November averaged 0·35 F.B.H.

Larvicidal control of *Simulium* in the dry season may prove more difficult than has been supposed, for it is noteworthy that an increase in the number of treatment points was also required in the scheme for control of *S. damnosum* on the Mayo Kebbi in Chad Territory (Taufflieb, 1955, 1956), where eradication was being attempted from an isolated focus some 34 miles in length along the Kebbi river by means of BHC applied against the larvae and also against the adults. In this scheme, three treatment points were used initially to deal with the 34-mile-long stretch of breeding ground, but when the 1955 results had proved unsatisfactory the number of treatment points was increased to five in the following year.

During the Abuja treatment periods, the rivers were extremely clear and free from silt or finely divided inorganic matter. It seems likely that the DDT would have been more effective for a greater distance had the rivers had a high turbidity. Noel-Buxton (1956) has recently found that DDT is an effective larvicide against *S. damnosum* at very low dosages when adsorbed on clay particles, and Barnley (1953) is convinced that a preferential affinity of the DDT solution for particles of silt in the water enabled the insecticide to be successful over 42 miles of the Victoria Nile, from the single treatment point at Napoleon Gulf to Lake Kyoga. Noel-Buxton (1956) suggests that the use of DDT adsorbed on clay of high colloidal quality enables the insecticide to be used successfully at much lower dosages than would otherwise be required, thus safeguarding against mortality

among fish; his tests showed that dosages exceeding 0·1 p.p.m. were dangerous to fish, but that dosages below 0·07 p.p.m. failed to destroy *Simulium* larvae. This makes the calculation of the correct quantity of DDT very critical to satisfy both requirements, and it is doubtful if the flow of the rivers can be assessed to a sufficient degree of accuracy. But the Abuja control project indicated no apparent effect upon fish with dosages between 0·3 p.p.m. and 2 p.p.m. over 30 minutes (the lowest and highest dosage rates at any application) providing the rivers were flowing uninterruptedly, but that some mortality occurred in the presence of impediments to the flow, which are thought to have caused local increases in concentration. Nevertheless, as Edwards (1956) has remarked, the application of insecticides to African rivers requires careful consideration in case it may cause a reduction in protein foodstuffs. In the Abuja area, fish is an important item in the diet of the Gwari people (B. M. Nicol, personal communication).

The Abuja control project has shown that area control of *S. damnosum* is feasible by treatment with DDT, applied as a larvicide, even in localities where networks of non-isolated breeding rivers exist, but that such treatment may require to be carried out annually if control is to be maintained, since reinfestation from untreated areas may be very rapid, especially if it can take place along river valleys rather than across country. In the Abuja project, the mean biting rate per hour over the whole *Simulium* season, in an area of some 1,200 sq. miles, with a population of 32,000 persons, was reduced from about 10 to 0·35 (96% reduction) in 1956, and to 1·71 (82% reduction) in 1957. It is not yet clear what this reduction will mean in relation to the incidence of onchocerciasis, since the effect of successful control would only be likely to show itself in the human population after an appreciable time, as a rise in the minimum age at which initial infection with *Onchocerca volvulus* occurred; but it seems unlikely that very much transmission could occur at the very low fly densities achieved as the result of treatment of the rivers with insecticide on the scale here described. The cost, however, of about £1,000 per annum required to produce control of the degree obtained is much more than a small native administration of the size of Abuja could sustain from local revenue.

The Abuja results are encouraging in that they indicate that some sort of control in difficult non-isolated foci is possible; but whether eradication from this type of area can be achieved is problematical, and Hughes (1956) does not believe that continent-wide insecticidal control will ever be possible as "*S. damnosum* can colonize tiny temporary streams". The latter assertion is certainly not true of Northern Nigeria or many other parts of Africa, where breeding is almost entirely confined to rivers. The statement of Gibbins & Loewenthal (1933) that "A study of the breeding habits of this species [*S. damnosum*] has proved the futility [*sic*] of attempting to attack the fly in its early stages" shows, however, that any prognostication of the future possibilities of control is unwise. But recent experience (*e.g.*, in the Mayo Kebbi control scheme) is beginning to show that the early successes against *S. damnosum* (*e.g.*, in Leopoldville and on the Victoria Nile) may not be repeated, and that in many areas, particularly West Africa, the effective control of this insect may prove extremely difficult.

Summary.

An experimental control project against *Simulium damnosum* Theo. in Northern Nigeria using DDT in diesel oil as a larvicide is described. A description, together with a map, is given of the project area, some 1,200 sq. miles in extent, with a population of 32,000 persons, and it is emphasised that this was selected to provide information on the feasibility of control in an area not isolated from other fly foci.

Methods used in applying the larvicide to the rivers, which had rocky beds with rapids and falls, and assessing the effects of treatment are discussed. Applications were made at prearranged treatment points, weekly, for a period of 12 weeks in the dry season of two successive years, 1956 and 1957, and the post-treatment density of adult fly was assessed and compared in a Table and in histograms, with that existing in the year prior to treatment.

In the first year, a mean dosage per application of 1·4 p.p.m. of p,p′DDT applied over 30 minutes (S.D. = 0·5 p.p.m.) at each of four treatment points resulted in the clearance of all breeding for a distance of 15–23 miles below these points, and a reduction of adult fly density in the area of 96 per cent. as compared with pre-treatment density. But reinfestation of cleared breeding grounds was found to be rapid, these becoming repopulated with immature stages within six months in spite of a mean wet-season fly density of only 0·35 flies per boy-hour.

In the second year, with application of 1 p.p.m. of p,p′DDT for 30 minutes, results were less successful than in the first, although three additional treatment points were used with the aim of controlling a greater distance than in the first year, adult density being only reduced by an estimated 82 per cent. of that before treatment in the first year. The reasons for this are discussed, and the lower degree of control is attributed to the partial failure of the insecticide to reach the breeding sites owing to the exceptionally low state of the rivers.

The fly-rounds used in assessing adult density and the pre-treatment breeding sites and the positions of the treatment points are shown on maps. Detailed data from the fly-rounds are given in an Appendix.

With the exception of slight mortality among fish, thought to be due to accidental impediments to the free downstream flow of the larvicide, no toxic effects on other organisms were observed.

The cost of treatment is given, and the results are discussed briefly in relation to the existing knowledge on control of *S. damnosum*. It is suggested that control by the application of larvicides in non-isolated foci is a practicable possibility, but that annual treatment might be necessary because of rapid re-establishment in cleared areas. The effect of control, of the degree obtained in this work, on the incidence of human onchocerciasis cannot yet be determined.

Acknowledgements.

I am especially grateful to Mrs. M. E. Crosskey, who during the course of this work was an assistant entomologist, for much general supervision of staff and treatments, for carrying out many of the river measurements, and for bearing most of the tedium of routine fly-rounds. I am grateful also to Dr. J. A. B. Nicholson for his prompt solutions to a number of administrative problems; to Mallam Sulaimanu Barau, Emir of Abuja, for his interest in the control work in his Emirate and for affording me the invaluable co-operation of the Abuja Native Administration; and to Dr. D. J. M. Mackenzie, late Director of Medical Services, Northern Nigeria, for his encouragement.

Thanks are due to the Chief Medical Adviser to the Government of Northern Nigeria for permission to offer this paper for publication.

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APPENDIX.

Density data for *Simulium damnosum* from individual catching points for the period June to November in each year. Fly-rounds and catching points are shown on map 2. An observation period represents a catching time of 15 minutes worked by one collector.

Fly-round number	Catching point	Number of flies caught: Pre-treatment 1955	Post-treatment 1956	Post-treatment 1957	Number of observation periods: Pre-treatment 1955	Post-treatment 1956	Post-treatment 1957	Mean number of flies per 10 observation periods*: Pre-treatment 1955	Post-treatment 1956	Post-treatment 1957
1	Iku Rapids ..	284	4	46	194	124	215	14·64	0·32	2·14
	Wuchichiri ..	76	5	91	25	120	215	30·40	0·42	4·23
	Rafin Kanya ..	37	7	160	25	122	216	14·80	0·57	7·41
	Post Office ..	33	0	54	24	114	220	13·75	0·00	2·45
	Workshop ..	103	18	80	33	114	220	31·21	1·58	3·64
	Farin Ruwa ..	136	11	146	33	114	218	41·21	0·96	6·70
	Ungwan Barebare	50	3	73	24	113	220	20·83	0·27	3·32
	G.R.A.** ..	93	8	62	24	128	219	38·75	0·63	2·83
	Madakin Iku ..	159	8	136	28	130	219	56·79	0·62	6·21
	Rafin Pa	217	6	118	29	130	219	74·83	0·46	5·39
2	Rafin Madugu ..	49	2	9	46	39	75	10·65	0·51	1·20
	Maje	21	2	7	21	39	75	10·00	0·51	0·93
	T. Mallam Karo	23	2	38	11	39	75	20·90	0·51	5·07
	Piakuchi	40	5	51	11	39	75	36·36	1·29	6·80
	Rafin Gwachipe ..	5	2	59	12	41	75	4·17	0·49	7·87
	Gwachipe	83	22	79	22	41	75	37·73	5·37	10·53
	Wagu	23	10	37	19	41	75	12·11	2·44	4·93
	Izom	20	0	19	30	41	75	6·67	0·00	2·53
3	Kwankashe ..	145	6	35	32	40	79	45·31	1·50	4·43
	Madalla	54	1	25	12	40	79	45·00	0·25	3·16
	Wuye	100	5	51	16	40	79	62·50	1·25	6·46
	Rafin Dede ..	120	1	69	18	40	79	66·67	0·25	8·74
	Gwagwa Plantation ..	21	1	15	11	40	79	19·09	0·25	1·89
	Gwagwa	13	0	12	13	40	79	10·00	0·00	1·52
	Karsana	14	1	16	8	32	79	17·50	0·31	2·03
	Dnako	7	1	40	10	32	79	7·00	0·31	5·06
	Jabi	3	7	44	8	32	79	3·75	2·19	5·57
	Wuse	0	0	3	8	30	79	0·00	0·00	0·38
4	Zuba	123	1	25	12	39	73	102·50	0·26	3·42
	Giri	38	4	44	15	31	73	25·33	1·29	6·03
	Gwagwalada ..	3	0	8	4	31	73	7·50	0·00	1·10
	Dabi	6	13	30	5	32	73	12·00	4·06	4·11
	Chukuku	12	21	60	4	32	67	30·00	6·56	8·96
	Ki	29	17	82	5	30	67	58·00	5·67	12·24
	Tsibiri	5	9	46	4	32	67	12·50	2·81	6·87
5	Tungan Buntu ..	25	1	9	28	40	73	8·93	0·25	1·23
	Kopa	10	1	18	25	40	73	4·00	0·25	2·47
	Ija	1	0	3	16	40	73	0·63	0·00	0·41
	Kuchiko	8	0	1	20	40	73	4·00	0·00	0·14
	Ungwan Shanu ..	0	0	3	10	33	73	0·00	0·00	0·41
	Diko	1	0	1	10	33	73	1·00	0·00	0·14
	Kayingwana ..	1	5	14	10	33	73	1·00	1·52	1·92
	Daku	25	2	65	10	35	73	25·00	0·57	8·90
Entire control area ..		2216	212	1984	925	2416	4648	23·96	0·88	4·27

* Density is expressed as the number of flies caught in 10 observation periods, and not in one period, in order to shift the point one place and make the figures more readily comprehensible at a glance. It should be noted that as one observation period is a catching time of 15 minutes worked by one collector (quarter boy-hour) ten observation periods represent a collecting time of 2·5 boy-hours. Hence the density in flies per boy-hour (F.B.H.) can be obtained by dividing the figures in the three right hand columns by 2·5, *i.e.*, multiplying by 2/5.

** Government Residential Area.

THE TERMITES OF THE SOLOMON ISLANDS.

By W. V. Harris * and E. S. Brown †

(Plates XXVII & XXVIII.)

This account of the termites of the British Solomon Islands Protectorate is based on the collections and field notes made by one of us (E.S.B.) during two years' residence on the islands. Additional information has been obtained from specimens in the collection of the British Museum (Nat. Hist.). A description of a new species from Guadalcanal Island has appeared elsewhere (Harris, 1958).

Previous references to the termites of this area have been brief. They include taxonomic papers by Hill (1927), Snyder (1925) and Harris (1957) and notes on their status as pests by Lever (1934 *a* & *b*, 1943, 1948). In this paper two species are added to the list. A key, together with illustrations of the soldiers of all species, are given to assist in identification.

The Solomon Islands lie some 500 miles to the east of New Guinea, in the latitudes 5° to 12° south of the Equator. They form part of the large chain of volcanic origin stretching from South-East Asia through Sumatra, Java and New Guinea to the New Hebrides. There are active volcanoes within the group. To the north lie the islands of the Bismarck Archipelago, while to the south are the New Hebrides. The Solomon Islands consist of seven major islands and many smaller ones, some of which are distant from the main body, *e.g.*, Rennell with Bellona 100 miles south of Guadalcanal, and Ontong Java 160 miles north-east of Santa Ysabel. Though administratively part of the British Solomon Islands Protectorate, the Santa Cruz Islands are regarded here as outliers of the New Hebrides.

The following termites are recorded from the Solomon Islands, all being represented in the present collection:—

Kalotermitidae.
- *Cryptotermes domesticus* (Haviland).
- *Neotermes sanctae-crucis* (Snyder).

Rhinotermitidae.
- *Coptotermes grandiceps* Snyder.
- *Coptotermes pamuae* Snyder.
- *Prorhinotermes inopinatus* Silvestri.
- *Schedorhinotermes browni* Harris.
- *Schedorhinotermes marjoriae* (Snyder).
- *Schedorhinotermes solomonensis* (Snyder).

Termitidae.
- *Microcerotermes biroi* (Desneux).
- *Termes odontomachus* (Desneux).
- *Nasutitermes novarum-hebridarum* (Holmgren).
- *Nasutitermes orientis* Snyder.

Of these 12 species, the domestic dry-wood termite *Cryptotermes domesticus* is too widely distributed in the Malayan, Papuan, Micronesian and Polynesian faunal areas to be of significance in the consideration of faunal relationships. Of

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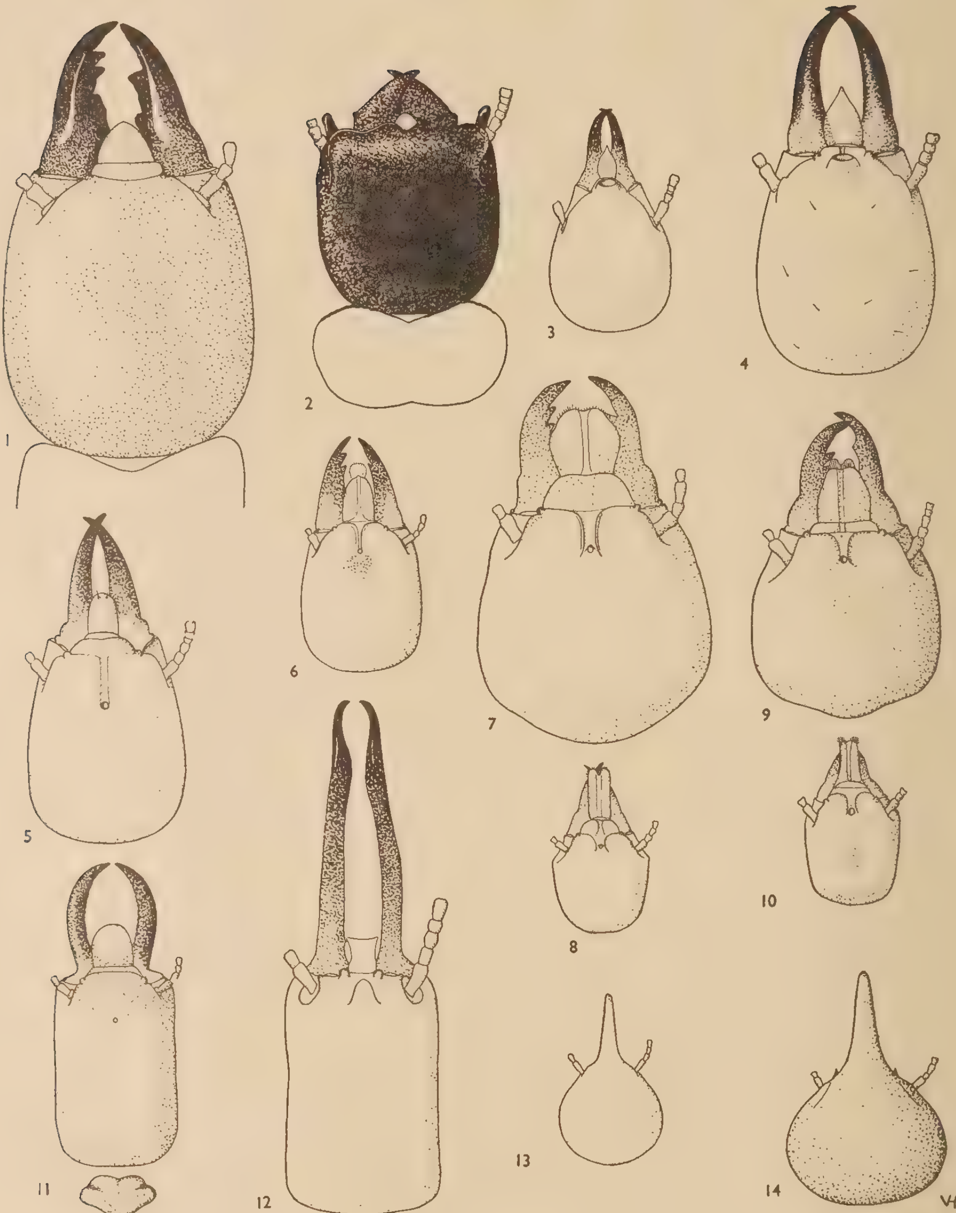

Figs. 1–14.—Heads of soldier castes of termites of the Solomon Islands. 1, *Neotermes sanctae-crucis*; 2, *Cryptotermes domesticus*; 3, *Coptotermes pamuae*; 4, *Coptotermes grandiceps*; 5, *Prorhinotermes inopinatus*; 6, *Schedorhinotermes browni*; 7, *Schedorhinotermes marjoriae*, large form; 8, *S. marjoriae*, small form; 9, *Schedorhinotermes solomonensis*, large form; 10, *S. solomonensis*, small form; 11, *Microcerotermes biroi*; 12, *Termes odontomachus*; 13, *Nasutitermes orientis*; 14, *Nasutitermes novarum-hebridarum*.

the 11 species remaining:— 5 species are known only from the Solomon Islands; 2 species are shared with the Santa Cruz Islands (probably part of the New Hebrides fauna); 2 species are shared with the Bismarck Archipelago and New Guinea; 1 species is common to the Bismarck Archipelago and the New Hebrides; 1 species is also found in the Polynesian and Micronesian fauna.

Field Key to the Soldier Termites.

This key is intended to be used in conjunction with the illustrations of soldier heads (figs. 1–14). Measurements, where given, are intended mainly to give some precision to the comparative terms " large " and " small ".

1. Head drawn out in front as a nose-like projection; no mandibles visible ...... *Nasutitermes* 2.
   Head not so drawn out; mandibles visible, pincer-like and large .... 3.
2. Head brown, nose conical with broad base; large .... *N. novarum-hebridarum* (fig. 14).
   Head yellow, nose near-cylindrical with narrow base; small species .... *N. orientis* (fig. 13).
3. Head pear-shaped with a large opening on projecting frontal area, in front of the antennal pits; mandibles sickle shaped without teeth ... *Coptotermes* 4.
   Head rectangular or ovoid, with frontal opening small, on flat frontal area behind the antennal pits .... 5.
4. Length of head and body 6·5 mm.; head long and narrow with long mandibles .... *C. grandiceps* (fig. 4).
   Length of head and body 3·5 mm.; head rounded with mandibles shorter in proportion .... *C. pamuae* (fig. 3).
5. Head cylindrical, hollowed out in front with rough surface, brown-black; mandibles short and stout (from furniture and timber) .... *Cryptotermes domesticus* (fig. 2).
   Head flattened, ovoid or rectangular .... 6.
6. Head rectangular, yellow, with fine, black, untoothed mandibles longer than the head itself; abdomen white; insect rather weak and fragile in appearance *Termes odontomachus* (fig. 12).
   Mandibles not longer than head, robust; abdomen yellow .... 7.
7. Mandibles with smooth inner margins; head oval; head and body yellow ...... *Prorhinotermes inopinatus* (fig. 5).
   Mandibles with teeth on inner margins .... 8.
8. Mandibles straight with sharply incurved tips, inner margins finely serrated ... *Microcerotermes biroi* (fig. 11).
   Mandibles curved from the base, inner margins with large teeth .... 9.
9. Large insect (12 mm.) with chestnut-brown head and short black mandibles, short pointed labrum and pronotum as wide as the head .... *Neotermes sanctae-crucis* (fig. 1).
   Small insect (not over 6 mm.) with yellow head, brown mandibles, long rectangular labrum, and pronotum not more than 2/3rds the width of the head *Schedorhinotermes* 10.
10. Soldiers of one size only; antennae with 13 segments ...... *S. browni* (fig. 6).
    Soldiers of two sizes (figs. 7 & 8, 9 & 10); antennae with 15–16 segments ... 11.
11. Head of larger soldiers deep orange, mandibles robust with first marginal tooth not more than 1/3rd of the way from tip of mandible .... *S. marjoriae* (fig. 7).
    Head of larger soldier yellow, mandibles less robust with first tooth more than 1/3rd of the way from tip of mandible .... *S. solomonensis* (fig. 9).

Records and Notes on Species.

For purposes of distributional records, the area is divided into main islands and groups as follows (these are arranged in alphabetical order under each species): Guadalcanal, Malaita, Nggela, Ontong Java (Lord Howe Atoll), Rennell and Bellona, Russell Islands, San Cristobal, Three Sisters, Western Group (including records from Arundel, Gizo, Kolombangara and Rendova), Ysabel. No

TABLE I.

Occurrence of species of termites in the main islands and island-groups in the British Solomon Islands.

	San Cristobal	Three Sisters	Guadalcanal	Malaita	Nggela	Ysabel	Russell Is.	Western Group	Rennell & Bellona	Ontong Java	Totals		
											C	F	B
Kalotermitidae													
Cryptotermes domesticus	—	—	B.2	+	—	—	—	B.1	—	—	—	—	3
Neotermes sanctae-crucis	+	—	F.2	—	—	—	—	—	+	F.1	—	3	—
Rhinotermitidae													
Coptotermes grandiceps ..	—	—	B.7	B.1	+	—	+	—	F.1	—	—	1	8
C. pamuae	+	—	B.9	B.2	—	—	—	—	—	—	—	—	11
Prorhinotermes inopinatus	—	+	—	+	—	—	—	—	F.2	—	—	2	—
Schedorhinotermes marjoriae	+ —	— —	C.8 B.1	— —	— —	— —	— —	C.1 —	— —	— —	9 —	— —	1 —
Sch. solomonensis ..	+ —	— —	F.1 B.1	+ —	— —	— —	— —	— —	— —	— —	— —	1 —	1 —
Sch. browni	—	—	F.1	—	—	—	—	—	—	—	—	1	—
Termitidae													
Microcerotermes biroi ..	+ — —	+ — —	C.31 F.2 B.2	— — —	+ — —	C.1 — —	C.2 — —	C.1 — —	C.1 F.1 —	— — —	36 — —	3 — —	2 — —
Termes odontomachus ..	—	—	F.3	—	—	—	—	+	—	—	—	3	—
Nasutitermes novarum-hebridarum ..	C.1 — —	C.2 — —	C.11 F.1 B.2	+ — —	+ — —	C.1 — —	C.1 — —	C.3 — —	C.1 — —	C.4 — —	24 — —	1 — —	2 — —
N. orientis	—	—	—	+	+	—	—	C.1	F.1	—	1	1	—
										Totals	70	16	28

C, F, B, indicate records from coconut palms or plantations, forest or outdoor habitats other than coconut plantations, and from houses or other buildings, respectively. Where there is a previous published record for an island from which no collections were made in the present work, it is indicated by a + sign.

collections have been made from Choiseul, the main island of New Georgia, nor from many of the smaller islands.

Records are only given where samples were actually collected and identified in the laboratory; the total number of samples so collected was 114. The relative abundance of different species, on a percentage basis, is thus roughly indicated by the numbers of records of each. However, this figure only gives an approximate idea, since collecting was biased in two directions: many more collections were made from Guadalcanal than from other islands (73% of the total), because more time was spent there, and insufficient time was available during brief visits to other islands to collect termites thoroughly; secondly, collecting was largely confined to coastal areas, and few samples were collected from inland forest at higher altitudes; furthermore, even in coastal areas, much more attention was paid to buildings and to coconut plantations than to other habitats.

All the records are summarised in Table I. For this purpose, habitats are grouped into three types: coconut palms or plantations (C); forest, or outdoor habitats other than coconut plantations (F); and houses or other buildings (B). This classification is useful primarily in showing which species are of economic importance; only those invading buildings are of any major importance; there is no evidence of any of the species frequenting coconut palms doing any harm, nor has damage to any other living plants been noted.

Notes on the nesting habits of each species are given where any details have been recorded.

Family Kalotermitidae—Dry-wood Termites

The Kalotermitidae are the most primitive living termites, with the exception of *Mastotermes darwiniensis* Froggatt of north-western Australia, and they have no special worker caste, but rely on the older nymphs for all domestic duties. The growth of the colony is slow and populations never reach the enormous numbers of other termites. They live entirely within the galleries in dead wood which have been excavated to provide food, and they have no need for any connection whatever with the soil. They digest their food with the aid of protozoa living in the lower intestine. Unlike other termites, their excreta are voided in the form of hard seed-like pellets, which provide a valuable diagnostic character when examining damaged timber. Most dry-wood termites are "wild", in the sense that they live in dead wood on growing trees, in ringed or felled trees left in the forest to season, or in fallen limbs and trunks. However some, more especially of the genus *Cryptotermes*, have become adapted to a "domestic" way of life, living in the woodwork of houses and in furniture, and have been carried by man in his belongings into many new countries.

Cryptotermes domesticus (Haviland).

Originally described by Haviland from Sarawak and Singapore (1898) it has been recorded under a variety of names from numerous localities in the Malayan, Papuan, Melanesian and Micronesian regions, as well as Siam, China and Formosa.

Guadalcanal: Honiara, 29.x.1955, from old piano; specimens include soldiers and numerous alates; 19.i.1956, from a desk in the Government Offices.

Western Group: Gizo, 16.xi.1955, from a table in the Medical Officer's house; nymphs only.

These three records (forming 2·6% of the total number of termite collections) are all from moveable articles of furniture. No dry-wood termites have so far been recorded from fixed building timbers, although their ultimate discovery in roof beams, floor boards and the like would seem to be only a matter of time. Information and specimens from Mr. P. G. Fenemore (*in litt.*, 1957) indicate that

C. domesticus is being found in increasing numbers on Guadalcanal, in furniture and fittings of houses. An illustration of dry-wood termite damage is given on Plate XXVIII, fig. 2.

Neotermes sanctae-crucis (Snyder).

This species was described by Snyder (1925) from the Santa Cruz Islands, and from Santa Anna Island adjacent to San Cristobal which is the nearest point in what is here regarded as the Solomon Islands. Harris (1957) gives Rennell Island and the New Hebrides as additional localities.

GUADALCANAL: Rua Sura Is., 17.vii.1955, in galleries running down the centre of a thin dead stump; Suta district, *c.* 4,000 ft., 27.vi.1956, in a standing dead trunk of a forest tree, about 5 in. in diameter. ONTONG JAVA: Leuaniua, 28.i.1955, from rotting log on ground.

There are only three records of this large species (2·6% of the total). None is associated with coconuts or with buildings, but all are from dead wood—a log on the ground in one case and standing dead stumps in the other two. The localities are varied, from an altitude of 4,000 ft. in the forest of Guadalcanal to sea-level on Rua Sura Is. and the flat coral atoll of Ontong Java. The species was also found at Santo and Vila in the New Hebrides, in standing dead trunks of cacao and *Erythrina*.

Family RHINOTERMITIDAE—Damp-wood Termites.

RHINOTERMITIDAE have large compact nests of a permanent nature, usually within chambers excavated in moist wood, such as the roots of an old tree well below the surface of the ground. Australia again provides an exception in that there the genus *Coptotermes* builds large mounds of earth. In South-east Asia, *Coptotermes formosanus* Shiraki, which is one of the major pests of buildings, is found in wooden boats, nesting in the moist timbers below the waterline, and foraging for suitable food all through the vessel. The RHINOTERMITIDAE digest their food with the aid of intestinal protozoa, as do the KALOTERMITIDAE, but their social organisation is more highly developed, they have a definite worker caste, and much larger populations. Characteristic of this family is the large gland in the head of the soldier and a corresponding large opening on the frontal area from which copious streams of viscous fluid are ejected in moments of stress, presumably of a defensive value. In the genus *Coptotermes*, the head is pear-shaped and the gland opening is carried well forward on the projecting frontal area. In *Schedorhinotermes*, the opening is on the flattened frontal area, but a long labrum, or upper lip, with a median groove carries the fluid forward to the tips of the mandibles.

Coptotermes grandiceps Snyder.

This species was described by Snyder (1925) from Tulagi. *C. froggatti* Light & Davis and *C. solomonensis* Snyder are placed in synonymy by Snyder (1949), and *grandiceps* is thus widely distributed within the Solomon Islands, including Rennell. It has been recorded in the Santa Cruz Islands by Hill (1942) but not, so far, elsewhere.

GUADALCANAL: Honiara, 16.vii.1954, from building (Post Office); 17.xi.1955, from building (Prison bakery); 14.iv.1956, from buildings (wooden pillars of Club at Rove, and Central Police Station); Kukum, 2.viii.1954, from house timbers; 1.xii.1954, alates swarming at light; 14.viii.1955, from house timbers. MALAITA: Auki, 24.v.1955, from cupboard in house. RENNELL and BELLONA: Lavanggu (Rennell), 23.xi.1955, from dead wood in forest; with alates.

There are nine records of this species (7·9% of the total), and eight of them are from buildings on Guadalcanal and Malaita; one of the latter is for alates

swarming at light, the remainder are from timber, in which extensive damage is frequently found (Pl. XXVIII, fig. 1). Entry into houses was effected by working up the interior of wooden pillars or along cracks in their surface, and through perforations in metal ant-caps. The only forest record was from dead wood on the ground on Rennell, and in such places it could doubtless be found widely if looked for.

Coptotermes pamuae Snyder.

The original description of this termite by Snyder (1925) from Pamua, San Cristobal Island, appears to be the only previous record.

GUADALCANAL: Honiara, 30.vi.1954, from house timbers; 19.vii.1954, from building (Government House Office); 4.viii.1954, from house timbers; 16.ix.1954, from building (safe in Treasury Office); with alates; 1.iii.1955, and 12.vii.1955, from house timbers; 5.xi.1955, from office in Secretariat, eating through piles of books; 17.xi.1955, from building (prison at Rove); Kukum, 4.viii.1954, from house timbers; 6.xi.1955, alates swarming at light. MALAITA: Auki, 24.v.1955, from house timbers (a new house only completed in February 1954); Malu'u, 22.viii.1956, from house timbers.

The 11 records (9·6% of the total) are all from buildings on Guadalcanal and Malaita; one is for alates swarming at light, and the others are all from damaged timber. Entry into houses was similar to that in the previous species; earthen runways were built up the surface of concrete pillars; these runways are often massive, and in one case had bridged across the overlap of a metal ant-cap. The damage is considerable, and one house on Malaita was heavily infested only 15 months after construction.

Prorhinotermes inopinatus Silvestri.

Though the Solomon Islands species of *Prorhinotermes* was originally considered to represent a new form, *solomonensis* Snyder, Snyder later (1949) placed it, together with his *P. manni* from Santa Cruz Islands, as a synonym of Silvestri's species described from Samoa, and subsequently found in Fiji, Tonga, Ellice Islands, the Marianas and Guam. Previous records from the Solomon Islands are from Auki, Malaita Island (Snyder, 1925) and Rennell Island (Harris, 1957).

RENNELL and BELLONA: Lavanggu (Rennell), 23.xi.1955, in dead stem of paw-paw (*Carica papaya*); Te'uhunggano (Rennell), 29.xi.1955, in rotting log on ground.

These two records (1·8% of the total) are both from Rennell, and in both cases from dead wood.

Schedorhinotermes browni Harris.

This species is considered to be new, and has been described by Harris (1958). It was found on only one occasion, and as this was one of the few collections made on the mountain slopes away from the cultivated areas it suggests that further search there might produce more new species.

GUADALCANAL: Gold Ridge, 22.iii.1955, under dying bark on trunk of forest tree (standing and still alive), *c.* 1,800 ft.

Schedorhinotermes marjoriae (Snyder).

Snyder (1925) described this termite from Ugi Island, off San Cristobal, since when it does not appear to have been recorded. The genus is well represented in the Malayan, Papuan and Australian regions as well as in Africa, and the number of species described, together with a marked tendency to variation within the species, makes identification difficult.

GUADALCANAL: Rua Vatu, 22.vi.1954, from roots of coconut palm; 20.xi.1954, from carton nest in roots of coconut; 24.xi.1954, under stems of creeper (*Epipremnum pinnatum* (L.) Engl.) on coconut trunk; 5.iv.1955, from carton nest on coconut trunk; 7.iv.1955, from mound nest in coconut plantation; 18.viii.1955, in roots of coconut; Aruligo, 17.xii.1954, in wet dead vegetation at foot of coconut trunk; Ilu, 17.iii.1955, in wooden pillar of house; Mamara, 30.vii.1955, in roots of coconut. WESTERN GROUP: Rendova, 8.x.1954, at foot of coconut palm.

There are 10 records (8·8% of the total) for this species. Only once was it taken in a building, from the wooden pillar of an old house at Ilu. In all other cases it was associated with coconut palms. Carton nests were found in three cases only, on the trunk or roots of the palm; a mound nest on the roots of one palm, about 6 in. from the trunk, was soft, black, fairly smooth externally and dome-shaped, about 9 in. in diameter. In other cases the termites were found amongst roots or dead vegetation at the foot of the trunk, or among stems of creepers higher up. Both small and large dimorphic forms of the soldiers and workers were usually present; the yellow colour of the soldiers is characteristic.

Schedorhinotermes solomonensis (Snyder).

This species was also described by Snyder (1925) from specimens collected at Pamua on San Cristobal Island, and at Auki, Malaita Island.

GUADALCANAL: Honiara, 30.vii.1954, in timber of small building, at ground level; Gold Ridge, 25.vi.1956, in log of rather dry dead wood in forest, *c.* 500 ft.

This is apparently rarer than the last species, and was only collected on two occasions (1·8% of the total). One record was for a building; the wooden floor was in direct contact with the ground, and the termites had remained at ground level and not penetrated upwards. The soldiers and workers are dimorphic as in *S. marjoriae*.

Family TERMITIDAE.

This is the largest family of the termites and embraces species with such great superficial variation in nest habit and in the shape of the soldier heads that a short definition is hardly possible. They do not have intestinal protozoa to assist with the digestion of wood, though some have a bacterial fauna which may help, and they have developed widely different methods of feeding, including the digestion of soil in quantity to extract the well-decomposed vegetable matter therein. Some build mounds on the surface of the ground, others make carton nests in trees, but always there is some connection with the earth. The termite fauna of the Solomon Islands is rich in individuals of this family, but poor in number of genera represented.

Microcerotermes biroi (Desneux).

Originally described by Desneux (1905) from north-east New Guinea, *M. biroi* is widely distributed over that island and New Britain, New Ireland, and the Solomon Islands south to Rennell. In addition, *M. peraffinis* Silvestri from Samoa is regarded by Snyder (1949) as synonymous.

GUADALCANAL: Mamara, 11.vi.1954, in carton nest on coconut trunk; Honiara, 19.vii.1954, from house timbers; Tenaru, 11.viii.1954, in carton nest on coconut trunk; with alates; 1.xii.1954, in carton nest on roots of coconut; 2.xii.1954, in carton nest 3–4 ft. up coconut trunk; with alates; 16.v.1955, from carton nest on roots of coconut; with alates; 3.viii.1955, in hole under perianth scales of a small coconut fruit on the ground; Rua Vatu, 22.xi.1954, in small, dead, erect tree-stump in coconut plantation; 23.xi.1954, in carton nest on coconut trunk; with alates; 5.iv.1955, in carton nest 4 ft. up coconut trunk; 6.iv.1955, on coconut trunk; 7.iv.1955, in hard mound nest on ground (1 ft. high); with alates; 8.iv.1955, from hard dome-shaped nest rising 15 in. from roots of coconut; with

alates; and also from another similar nest; 8.xi.1955, from five carton nests from among many similar ones on coconut trunks, mainly about 4 ft. from the ground; with alates in some cases; 9.xi.1955, in carton nest on coconut trunk, and from hard mound nest rising from roots of coconut; with alates; also from small fallen coconut fruits on the ground, into which they had bored; 10.xi.1955, from two mound nests on ground; with alates; Aruligo, 17.xii.1954, in roots of coconut; Kukum, 4.iii.1955, on coconut trunks (three samples); 17.i.1956, from two carton nests 3 ft. up coconut trunks, and also from a mound nest on roots of coconut; 10.iv.1956, on coconut trunk; Ilu, 17.iii.1955, in house timbers; Gold Ridge, 22.iii.1955, in runways on trunk of forest tree between Tsarivonga and Tinahula rivers; 30.vi.1956, from mound nest on ground in forest. RUSSELL ISLANDS: Butete, 5.ix.1955, in mound nest on ground; Fai Ami, 9.ix.1955, on coconut trunk; with alates. RENNELL and BELLONA: Lavanggu (Rennell), 23.xi.1955, in rotten wood; Te'uhunggano (Rennell), 26.xi.1955, from carton galleries on coconut trunks at the beach-head. WESTERN GROUP: Kolombangara (Karikana Estate), 14.x.1954, from mound nest on ground in coconut plantation; with alates. YSABEL: Gatere, 19.ii.1956, in carton nest 4 ft. up coconut trunk.

This species accounts for no less than 41 records (35·9% of the total). Of the collections, 36 (88%) are from coconut plantations where, on Guadalcanal at all events, it is the really characteristic species and the carton nests it constructs on the trunks (Pl. XXVII, fig. 1) are often a very prominent feature of a plantation. Only twice was it found in buildings, once in one end of an old disused house at Ilu and once in a house in Honiara, where infestation did not appear to be heavy or extensive. Lever (1934*b*) states that this species feeds on vegetable refuse as opposed to timber. The only "forest" records were not far from the coast.

The carton nests are usually associated with coconut trunks, and are found either on the trunks up to four or five ft. above ground level (Pl. XXVII, fig. 1), or on the ground; in the latter case they are either built out from among the aerial roots (Pl. XXVII, fig. 2) or else are within a few feet of the base of the trunk. A nest on the ground usually takes the form of an erect mound about 12–15 in. high and 9–12 in. across, and the surface is fairly smooth; nests further up the trunk are about 4–6 in. thick and are usually oblong, extending 18 in. to over 3 ft. up and down the trunk; numerous protuberances often give them a rougher surface than in the ground nests; strong carton runways radiate out from the nest both up and down the trunk. These runways can be built out perpendicularly from the surface as tubes; on one occasion at Kukum, certain experiments involved painting grease bands, 6–9 in. broad, round the trunks of palms to act as a barrier to ants, all runways and creepers having first been cleaned off the trunk. On one or two palms *Microcerotermes* was also present and, like the ants, was unable to cross the grease band until the obstacle was surmounted by extending the runways out into the air as tubes and down over the grease band, often without making any contact with it; the rate of construction of these tubes was of the order of one inch in 24 hours.

In the forest locality between the Tsarivonga and Tinahula rivers there were small tubular turrets at intervals along the runways, protruding perpendicularly about ¼ in. into the air; these were not noticed in coconut plantations

The characteristic small, black, winged adults are frequently to be seen in the nests; they were found in January, April, May, August, October, November and December and doubtless occur throughout the year. Queens are about ¾ in. long and are readily found in the carton nest (Pl. XXVII, figs. 3, 4).

Termes odontomachus (Desneux).

Like the previous termite, this species was described by Desneux (1905) from New Guinea. An earlier record of "*Microtermes* (*Protocapritermes*) *krisiformis*

(cited as *trisiformis*) Frogg.'' from the Western Group (Lever, 1943) is now found to have been based on a misidentification, and refers to this species.

GUADALCANAL: Gold Ridge, 22.iii.1955, from mound nest on the ground in the forest at about 1,000 ft., just north of the Tinahula river; with alates; 25.vi.1956, from two separate mound nests on the ground in the same area, at about 1,000–1,500 ft.

Only three samples of this species were collected (2·6% of the total). All were from the Guadalcanal forest at altitudes of 1,000 ft. or higher; it may well be common at higher altitudes, where little termite collecting was done. All the samples were taken from smooth, dome-shaped, rounded mound nests about 9 in. high on the forest floor.

Nasutitermes novarum-hebridarum (Holmgren).

The sub-family NASUTITERMITINAE, whose soldiers have characteristic heads drawn out in front to form a long pointed nose, and jaws so small as to be almost unnoticeable, has a large number of genera and species throughout the tropics. *N. novarum-hebridarum* was described by Holmgren & Holmgren (1915) from the New Hebrides, and is of interest in being one of the few termites which appear to be restricted to the New Hebrides–Solomon Islands–New Britain and New Ireland chain of islands. *N. oceanicum* Snyder from the Santa Cruz Islands and *Eutermes yandiniensis* Hill from the Solomon Islands and Bismarck Archipelago are synonyms.

GUADALCANAL: Rua Vatu, 22.vi.1954, from carton nest on coconut trunk; 22.xi.1954, from carton nest on coconut trunk; with alates; 7.iv.1955, on coconut trunk; with alates; Tenaru, 5.viii.1954, from carton runways on coconut trunk; 18.xi.1954, on coconut trunk; Mamara, 27.viii.1954, on coconut trunk; Kukum, 7.xii.1954, from carton nest on coconut trunk; with alates; 4.iii.1955, on two separate coconut trunks; 28.iii.1955, as prey of the ant *Oecophylla smaragdina* (F.), on coconut trunk; 17.i.1956, from carton nest on roots of coconut; Honiara, 17.xi.1955, from timber in two prison wards at Rove; Tsarivonga river, 19.iii.1955, from runways on trunk of forest tree. ONTONG JAVA: Kapae, 29.i.1955, from runway on coconut trunk; Avaha, 2.ii.1955, from runways on two coconut trunks, with a small carton nest in one case; another sample from Ontong Java, without detailed data. RENNELL and BELLONA: 21.xi.1955, from small carton nest on coconut trunk (Bellona). RUSSELL ISLANDS: Somata, 7.ix.1955, in roots of coconut. SAN CRISTOBAL: Boroni, 14.x.1955, at base of coconut trunk. THREE SISTERS: Malau Paina, 25.iv.1955, in roots of coconut, with carton runways up trunk; Malau Lalo, 26.iv.1955, from carton galleries on coconut trunk. WESTERN GROUP: Kolombangara (Karikana Estate), 1.x.1954, at foot of coconut palm; Rendova, 7.x.1954, and 8.x.1954, at foot of coconut palms. YSABEL: Fara Is., 9.ii.1955, in carton nest at base of coconut trunk.

While *Microcerotermes biroi* is the most abundant termite in coconut plantations on Guadalcanal, the present species is also very common in similar situations and appears to be more widespread, for it was collected twice as often in islands other than Guadalcanal. There were 27 collections altogether (23·6% of the total), of which 24 were from coconut plantations. The only occasion it was found in buildings was in the prison at Honiara, where it occurred in two of the wards although *Coptotermes grandiceps* and *C. pamuae*, the usual household species, were present in others. Lever (1934*b*) classes it with *Microcerotermes biroi* as feeding on vegetable refuse as opposed to timber. The only " forest " record is for a locality not far from the coast on Guadalcanal.

On coconut trunks this species is often found in runways without any conspicuous carton nest; nests have been found, however, both on the roots at the base and farther up the trunk; those which have been identified as belonging to

this species have had relatively smooth surfaces without the marked protuberances often found in the case of *M. biroi*. Alates have been found in January, April, November and December; they are much larger than those of *M. biroi*, and have greyish wings instead of black ones as in that species.

Nasutitermes orientis Snyder.

This species was described by Snyder (1925) from Auki, Malaita Island, with a variety *tulagiensis* from Tulagi Island. The specimens in the present collection appear to belong to the typical form, as do those recently examined from Rennell (Harris, 1955).

RENNELL and BELLONA: Lavanggu (Rennell), 23.xi.1955, in rotten wood. WESTERN GROUP: Arundel, 4.x.1954, at foot of coconut palm.

There are only two records for this species (1·8% of the total).

TERMITE DAMAGE TO BUILDINGS, AND NOTES ON CONTROL MEASURES.

From the records of the present collection the occurrence of species of termites that damage buildings may be summarised as follows:—

	Records Total	Records Buildings
Cryptotermes domesticus	3	3 or 100 per cent.
Neotermes sanctae-crucis	3	0
Coptotermes spp.	20	19 ,, 95 ,, ,,
Prorhinotermes inopinatus	2	0
Schedorhinotermes spp.	13	2 ,, 15 ,, ,,
Microcerotermes biroi	41	2 ,, 5 ,, ,,
Termes odontomachus	3	0
Nasutitermes spp.	29	2 ,, 7 ,, ,,

Coptotermes spp. and *Cryptotermes domesticus* are the only termites for which all or nearly all the records are from buildings. *Coptotermes* was recorded much the more frequently and the two species, *C. grandiceps* and *C. pamuae*, seem to be of approximately equal importance (see Table I for further details). Although *Cryptotermes* was recorded only a few times, more recent information confirms that it is, nevertheless, of major potential importance. As "dry-wood" termites, they can live in dry timbers without maintaining any contact with the soil, while all the other species, including *Coptotermes*, require more or less constant communication with the soil, and therefore offer a wider range of possibilities for control methods. Of these latter termites that are present in the Solomon Islands, only the species of *Coptotermes* are considered serious pests; others, such as *Schedorhinotermes marjoriae* and *Sch. solomonensis*, *Nasutitermes novarum-hebridarum* and to a lesser extent *Microcerotermes biroi*, appear relatively unimportant, but evidence is not sufficient to state that they are not potentially more harmful; it is possible that they might prove more troublesome in certain circumstances, such as in the absence of competition from *Coptotermes*.

In considering means of protection of buildings against termites (which has all too frequently been either inefficient or completely neglected in the past), one decision of fundamental importance has to be taken. Is complete reliance to be placed in protection from the ground, which in theory is all that is necessary against ground-dwelling termites generally, provided it is efficiently carried out? Or are protective measures to be taken also against dry-wood species, which can infest a building from the air and maintain existence in it without any communication with the soil? The first involves only correct house construction, while the second involves impregnation of the building timbers with a suitable poison.

It may be argued that since, in the Solomon Islands, dry-wood termites

(*Cryptotermes*) have been recorded only in movable articles of furniture and not in building timbers, they can be left out of account, and correct house construction is all that one need worry about. This is, however, an unsafe assumption; the fact that *Cryptotermes* exists at all is sufficient to make it imperative to guard against it, for there seems no good reason why it should not become more widespread; there are recent records from the Honiara district and Gizo, and *C. domesticus* has been reported from Tulagi in the past. If competition from damp-wood species is reduced by more efficient house construction, there is every reason to expect that *Cryptotermes* will increase; at Tarawa, in the Gilbert Islands, where damp-wood termites apparently do not occur, *Cryptotermes* is now a very serious pest. There is also the point that efficient impregnation protects timbers against damp-wood termites and wood-boring beetles as well and thus has a wider function. It is therefore unwise to neglect timber impregnation. If it is adopted, however, this does not imply that protective building construction can be neglected, because local instances of faulty impregnation would almost certainly occur and would open the door to the more abundant soil termites which are always ready to discover a weak point. Maximum security can therefore only be attained by carrying out both methods of protection.

As regards house construction, this is not the place to discuss all the details of method, which are described at length in special works (*e.g.*, Anon., 1950; MacGregor, 1950; Harris, 1955). It will be sufficient to point out certain aspects of special application to the Solomon Islands, and to call attention to some of the principal defects which have come to light in house construction in recent years.

The first essential is to raise the house either on pillars, or on a solid concrete block. Pillars should be of solid concrete, with the surface smooth and free from crevices; occasionally pre-cast hollow cement bricks are used for building pillars, and in some cases these have been unfilled or only filled with loose masonry, providing *Coptotermes* with internal runways up which it can pass unobserved; this possibility can be eliminated by filling the cavities carefully with concrete. The pillars should be high enough to facilitate examination by an inspector under the house; houses are often built on sloping ground rising steeply from the sea, and the pillars on the uphill side may then be too short to allow adequate inspection; this can be avoided if the ground is levelled before the house is built.

Pillars alone without regular inspection are inadequate since *Coptotermes* will build carton runways up their outer surface and enter the timbers above; no insecticide treatment has been found to prevent this indefinitely. Metal termite shields between the pillars and the floor of the house are therefore desirable. The method of construction of these is illustrated (Pl. XXVIII, fig. 4); important points to note are that the down-turned flange must be broad enough, and the corners must be crimped instead of cutting the metal and overlapping the cut edges, for the latter procedure will almost certainly leave an aperture large enough for the passage of termites. *Coptotermes pamuae* was found in one instance to have filled up the angle between flange and pillar with carton material and thus created a bridge enabling it to pass round the outside; an overlapping flange of 3–4 in. width would have prevented this. Another defect of very frequent occurrence in the metal shields results from piercing their centres for the passage of an iron shaft to secure the floor joists, which invariably leaves a gap sufficient to admit termites. This can be prevented by applying a substantial layer of pitch between the top of the pillar and the metal shield. The pitch will be forced into any crevices by the weight of the house and so block them.

Some of the buildings in Honiara have solid concrete floors. Provided they are sound and that any danger spots round the margin can be inspected, they are very satisfactory. In some buildings, however, the protection has been sacrificed

by supporting the roof with wooden pillars which have been sunk right through the concrete and into the soil ! *Coptotermes grandiceps* was quick to find these loopholes. Another way in which concrete bases have been rendered ineffective is by the building of wooden steps and lean-to garages of timber, structures which are in contact with both soil and the timbers of the house; in the example illustrated (Pl. XXVIII, fig. 3), *C. grandiceps* is seen using a lean-to shed to by-pass the concrete base of a house. Both this species and *C. pamuae* are quick at discovering such flaws; a house on Malaita was found to be badly infested by *C. pamuae* 15 months after construction.

The question of suitable poisons for impregnation of timber is a technical one, and will not be dealt with here except to call attention to some factors of local significance. A most important factor is the high cost of freight, making bulky materials costly to obtain from outside the islands. This is a drawback to pentachlorophenol (although it would doubtless prove effective, as it has done in South Africa), because it requires organic solvents; also since more than one solvent would be required to impregnate timber wanted for different purposes, it would involve complications with the limited impregnation equipment available. The same disadvantages would apply to creosote, which in any case could only be used for external woodwork which is not going to be painted.

Some kind of water-soluble substance which is not bulky, and can be made up locally without importing special solvents, is therefore strongly indicated. This still leaves a wide choice. Preference should be given to materials which become highly fixed in the wood—especially important for outdoor work because of the heavy rainfall. Further, selection should also take into account the relative merits of highly poisonous arsenical materials, which would involve hazards with unskilled local labour used in the process of impregnation, and of less poisonous materials based on copper sulphate or chromates.

Summary.

Twelve species of termites occurring in the British Solomon Islands Protectorate are listed, and an illustrated key to their soldier castes is provided. An analysis of the 114 records has been made in order to indicate, in a general way, the relative abundance of the various species. Notes are given on distribution within the islands, on habitats and nests, and on the occurrence of termites on coconut palms and in buildings. Damage to buildings is discussed and suggestions made for control measures applicable to local conditions.

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FIG. 1. Carton nest on side of coconut palm, runways seen on smooth bark leading to the ground below and upwards in search of dead woody matter.

FIG. 2. Similar nest on coconut palm at ground level.

FIG. 3. Vertical section of fig. 2, to show internal structure of nest.

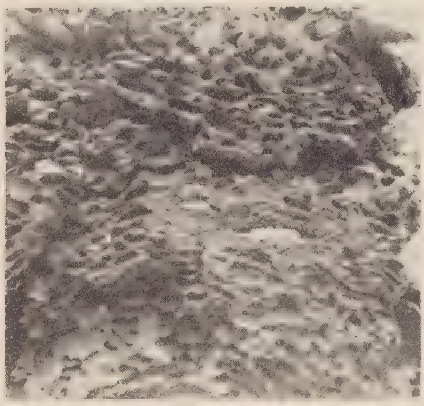

FIG. 4. Close-up of queen in royal cell surrounded by nymphs and by workers already engaged in repairing the damaged cell.

NESTS OF *MICROCEROTERMES BIROI* ON GUADALCANAL.

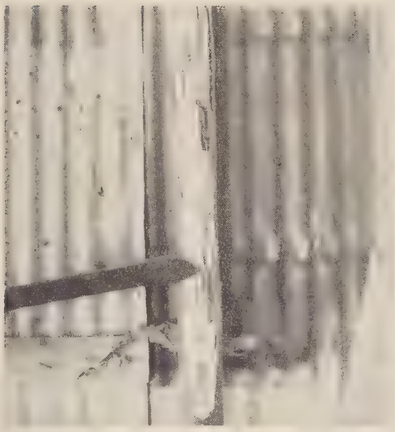

FIG. 1. Roof pole attacked by *Coptotermes grandiceps.*

FIG. 2. Part of a piece of furniture infested by *Cryptotermes domesticus.*

FIG. 3. Careless construction of lean-to shed allows *Coptotermes* to reach walls of house above the termite-proof concrete base, *via* timber in contact with the soil.

FIG. 4. Metal shields on top of concrete pillars protect new building from ground-dwelling termites.

TERMITE DAMAGE TO BUILDINGS ON GUADALCANAL.

DIAPAUSE AND THE REGULATION OF DEVELOPMENT IN *ANTHRENUS VERBASCI* (L.) (COL., DERMESTIDAE).

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(Plate XXIX.)

Contents.

Anthrenus verbasci (L.), commonly called the Varied Carpet Beetle, is widely distributed in temperate regions. The larvae feed on materials of animal origin and are a major pest of dried insect collections and of the silk industry where they feed on the cocoons and dried pupae of silkworms. The larvae are common in house-sparrow nests, which form an important source of household infestations (Woodroffe & Southgate, 1954).

There is very little detailed information on the development of *A. verbasci*. The main works are those of Kalandadze (1927), Yokoyama (1929), Kunike (1938, 1939), Yamada (1940), Griswold (1941) and Kuwana (1951). A detailed review of the literature is given by Hinton (1945), who describes the adults and larvae, and includes them in a key to the Dermestidae associated with stored products. The main points of interest and the later work of Kuwana will be discussed and compared with the results obtained in the present study.

The life-cycle of *A. verbasci* is closely tied to the seasons. Adult beetles are found in spring on many species of creamy white flowers, where they mate and feed on pollen and nectar. Probably most eggs are laid in birds' nests in the eaves and attics of buildings, but some are laid on woollen materials and on many other products of animal origin. The larvae grow during the summer months and enter diapause during the winter, taking one, two or more years to develop. In the autumn in which they are fully grown, many leave the attic or feeding place and wander into the interior of the building, where they cause damage to many household goods. Pupation occurs in the early spring and the emergent

adults, after a period of inactivity, fly to the windows and out on to flowers. Stages in the life-history are shown in Plate XXIX, figs. 1–6.

Materials and Method of Culture.

Cultures were started with adults of unknown age collected from flowers during May, June and July 1950. These were sub-cultured and, in addition, new cultures with wild adults were started in the succeeding years. The cultures were maintained in 7-lb. jars with muslin covers. The food for the larvae was made up of a two to one mixture of fishmeal and debittered yeast (Glaxo Laboratories), a small quantity of cholesterol, a few dead insects, some wool and some flannel. The cholesterol and insects were ground together with a pestle and mortar and then thoroughly mixed with the yeast and fishmeal. The wool was previously treated with cholesterol and yeast (Rawle, 1951) by soaking it in a warm solution of 10 g. cholesterol and 100 g. yeast to 1 litre of water. The wool was then squeezed until the weight of the hank was twice that of the dry hank. The hanks were dried and a small quantity added to each jar. A piece of woollen flannel about 10 cm. × 20 cm. was also added. The cultures were kept at 25°C., 70 per cent. R.H. for the first year, but later, when the preliminary studies showed that 20°C. was nearer their optimum than 25°C., they were placed at 20°C., 70 per cent. R.H. The insects were reared in continuous darkness. Under these conditions the cultures have been successfully maintained for nearly seven years.

Incubation Period of the Egg.

Adults were allowed to lay in petri dishes lined with dark-coloured woollen cloth (100 adults/dish). Eggs were removed daily with a paint brush and placed in 2″ × 1″ tubes with muslin-covered bored corks. Daily records, as far as possible taken at the same hour, were kept of the number of larvae emerging.

The incubation period decreased with rise in temperature (fig. 1). At 10°C. (30, 70 and 90% R.H.), the eggs showed no signs of development after exposure for 12 months, and, at 35°C. (30, 70 and 90% R.H.), the eggs shrivelled and none hatched. Relative humidity had little effect upon the length of the incubation period, although there was a slight tendency for the period to be shorter at the higher humidities.

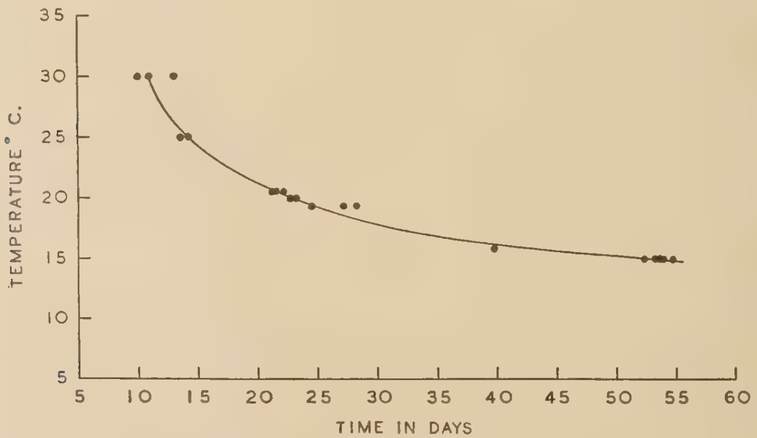

Fig. 1.—Effect of temperature on the length of the incubation period of the egg.

The first incubation experiment was carried out in July 1951 with eggs laid by adults collected from flowers. The experiment was repeated in November 1951 with eggs laid by adults from the cultures. The incubation periods in the second experiment were rather longer than those in the first, especially at the lower temperatures of 15 and 20°C. The most reasonable explanation for this discrepancy was that the two groups of eggs had experienced different temperatures.

TABLE I.

Effect of temperature and relative humidity on the incubation period.

Adults from flowers						Adults from cultures					
Temp. (°C.)	R.H. (%)	No. of eggs	% hatched	Incubation period (days) Mean	Range	Temp. (°C.)	R.H. (%)	No. of eggs	% hatched	Incubation period (days) Mean	Range
—		—		—		15·0	30	40	52·5	53·7	51–57
—		—		—		15·0	70	40	52·5	53·2	50–57
15·0	70	128	71·9	53·5	51–56	15·0	70	119	57·1	54·6	52–57
15·8	90	25	100·0	39·7	39–41	15·0	90	20	65·0	52·3	50–55
20·5	30	25	80·0	22·1	21–23	19·3	30	20	50·0	28·2	27–29
20·5	70	20	80·0	21·5	21–22	19·3	70	20	85·0	27·1	25–29
20·0	70	100	62·0	23·4	23–25	20·0	70	120	94·2	22·9	22–26
20·5	90	25	60·0	21·2	22–22	19·3	90	20	65·0	24·5	24–25
25·0	30	25	72·0	14·1	13–15	25·0	30	20	90·0	14·1	14–15
25·0	70	25	64·0	13·6	12–15	25·0	70	20	85·0	14·1	14–15
25·0	70	125	72·0	14·3	14–15	25·0	70	150	75·3	14·1	14–15
—		—		—		25·0	90	40	77·5	14·2	13–17
30·0	30	25	40·0	13·0	13–13	30·0	30	20	85·0	13·0	13–13
30·0	70	25	52·0	11·0	11–11	30·0	70	20	55·0	10·0	10–11
—		—		—		30·0	90	40	70·0	11·0	10–11

A check was made of the thermograph charts and the mean temperatures actually experienced by the eggs in both experiments were calculated. These corrected values are given with the results in Table I. The higher temperatures experienced during July and the lower ones during November accounted for most of the variation. A further experiment carried out in August 1953, with wild and laboratory adults simultaneously, confirmed that there was no real difference in the length of the incubation period for eggs from wild or laboratory stocks. The mean percentage hatch for the two groups was similar, 68·5 per cent. for eggs laid by adults from flowers and 70·6 per cent. for eggs laid by adults from cultures.

Larval Development.

Eggs laid by 100–200 adults were collected and incubated at 20°C., 70 per cent. R.H. The experiments were started with these newly emerged larvae, 0–1 day old, which were placed and reared individually in 2″ × ½″ glass tubes, closed by perforated corks and a double layer of muslin. The foodstuff was similar to that on which the cultures were maintained (p. 752). Development was studied under natural, constant and alternating conditions as follows:—

(a) Three grades of naturally fluctuating temperature, humidity and light, which were obtained by exposing the larvae in three places in the grounds of the laboratory, (1) in a cupboard in an unheated storage hut, (2) in an unheated summer-house and (3) in a Stevenson screen. Thermohygrograph records were

kept of the conditions in each place. The intensity of illumination in each place was measured with an Evans Electroselenium cell. At noon on a bright but sunless day in June, the intensities were as follows:— in the hut, less than 0·1 ft.-candles, in the summer-house, 20·0 ft.-candles and in the screen, 6·0 ft.-candles. The intensities varied diurnally, seasonally and with prevailing weather conditions.

(b) Constant temperatures of 5, 10, 15, 17·5, 20, 22·5 and 25°C., with constant relative humidities of 30, 70 and 90 per cent. for each temperature, were obtained by the use of refrigerators, incubators and controlled-temperature rooms. Relative humidity was controlled by potash solutions (Solomon, 1951). These larvae were kept in darkness except during periods of observation.

(c) Three grades of controlled alternating temperature were obtained by the use of three small incubators, designed by Mr. T. A. Oxley. For the present purpose they were set to alternate each day between 18 and 23, 18 and 28 and 18 and 33°C. The temperature was thermostatically controlled and during the night (9 p.m.–9 a.m.) was held at 18°C. At 9 a.m., heaters, controlled by a time switch, raised the temperature to the required level of 23, 28 or 33°C. The change-over from 18°C. to the higher temperature and *vice versa* took about half an hour. The incubators were too small to take a thermohygrograph and no record was kept of the relative humidity. The humidity of the air surrounding the incubators was between 80 and 90 per cent. R.H. These larvae were kept in darkness except during periods of observation.

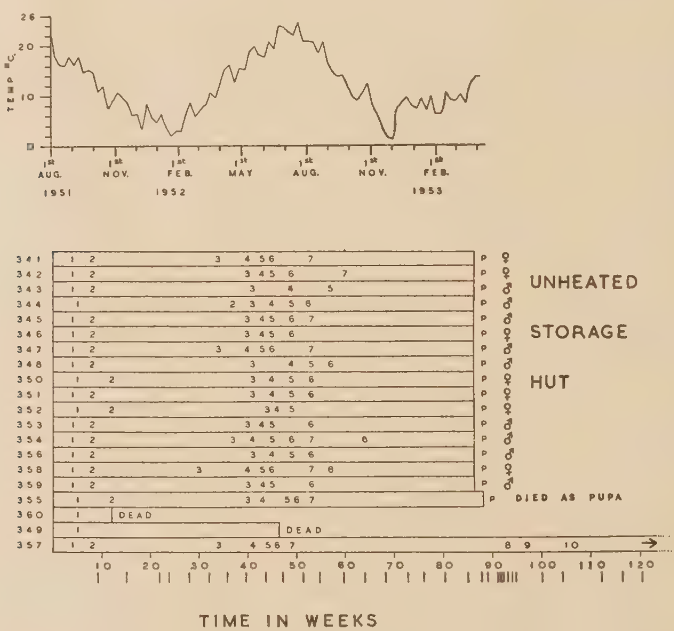

Fig. 2.—Larval development in conditions of fluctuating temperature and humidity in a cupboard in an unheated storage hut, showing the rhythm of moulting for individuals. Each moult is numbered, and the time of moult, pupation (P) or death is given as the mean of the observation times before and after the event. Where two or more moults occurred between observations, they have been evenly spaced. The vertical lines below the figure indicate the times of observation. Above: mean weekly temperatures in the cupboard. No. 357 died, without moulting again, at the 140th week.

The larvae were observed about every four weeks (the exact times of observations are shown on the figures) when cast skins present were removed and noted. It was exceedingly difficult to find the first-instar larvae and their cast skins, for the very slightest movement of air was sufficient to blow away a first-moult skin. If a larva appeared to be the same size as one from which the cast skin had been found, then it was credited with having moulted. In general, this inaccuracy concerned only the first-moult skins and occasionally a second-moult skin, whilst later skins were always found.

Larval development in conditions of fluctuating temperature and humidity.

In field conditions, the rate of larval development fluctuated with the seasons in a regular manner. A short period of activity during the summer months, from

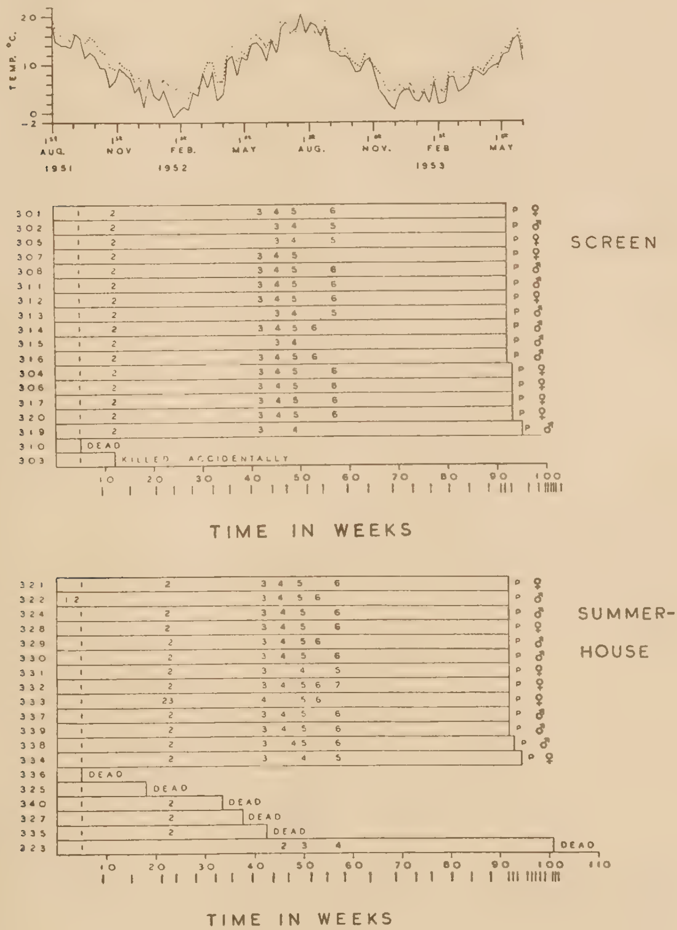

Fig. 3.—Larval development in conditions of fluctuating temperature and humidity in a Stevenson screen and a summer-house, showing the rhythm of moulting for individuals. Above: mean weekly temperatures in the screen, ————; and in the summer-house, ·························.
For explanation of symbols, see fig. 2.

about the beginning of May to the end of August, was followed by a long period of rest during the autumn and winter months (Sept.–April).

The field experiments carried out in unheated outhouses (the storage hut and summer-house) and in the Stevenson screen were started on 1st August 1951, with larvae the direct progeny of beetles collected from flowers.

The larvae developed for a short period during the end of that summer, reaching the second or third instar. They rested in this instar for the winter. Activity recommenced about the middle of May 1952 (about 1st May in the storage hut) and growth proceeded during the summer, the larvae becoming fully grown. The final resting period, as fully grown larvae, started about the end of August 1952 (end of July 1952 in the storage hut) and lasted until the end of April 1953 (the middle of March 1953 in the storage hut) when all the larvae pupated within five days. Thus larval development had taken nearly two years (figs. 2 & 3).

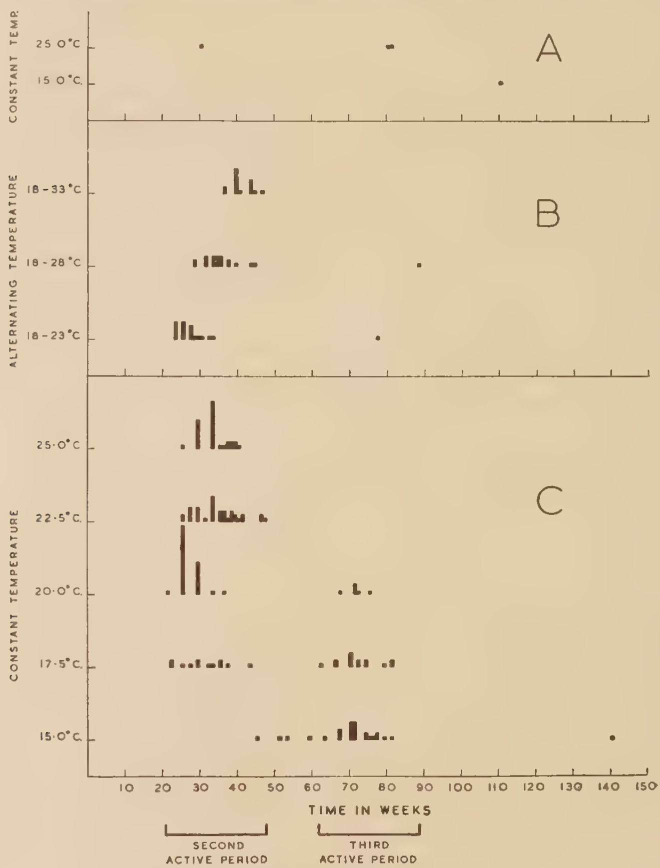

Fig. 4.—Frequency of pupation times when larval development has taken place in each of the following conditions. A, in constant conditions of temperature and at controlled humidity (70% R.H.) with malnutrition. B, in alternating conditions of temperature and at uncontrolled humidity. C, in constant conditions of temperature and humidity; for each temperature, development took place at 30% and 70% R.H., and, at 20·0°C., three individuals are included that pupated at 90% R.H. A black square represents the time of pupation, to the nearest week, of one individual.

This pattern of development may be conveniently summarised as follows:—moulting, rest, moulting, rest, pupation, *i.e.*, m—m—p.

The boundaries of these active and resting periods in the summer-house and screen (fig. 3) were very precise. There was virtually no variation among the individuals in either place and the rates of development in the two sites were similar. In the storage hut (fig. 2) by comparison with the summer-house and screen there was considerable variation among individuals and the active periods occurred earlier in the year, *i.e.*, 1st May to end of July as compared with the middle of May to end of August. The main difference in physical conditions between these places concerned temperature and light. The larvae in the storage hut were in a cupboard which buffered the extreme temperatures and kept out the light, whilst the larvae in the summer-house and the screen experienced extreme temperature conditions and diffuse daylight.

Larval development in conditions of constant temperature and humidity.

It has been shown above that the rate of larval development under field conditions fluctuated with the seasons. When larvae were reared under constant conditions it was found that there was a basic rhythm of alternate moulting and resting periods persisting over at least 80 weeks, during which time there were three periods of activity and two of rest. The lengths of these periods were not the same as those occurring under field conditions. Their boundaries were determined in the following manner. From the frequency histogram of pupation times (fig. 4) it can be seen that there were two periods during which most of the

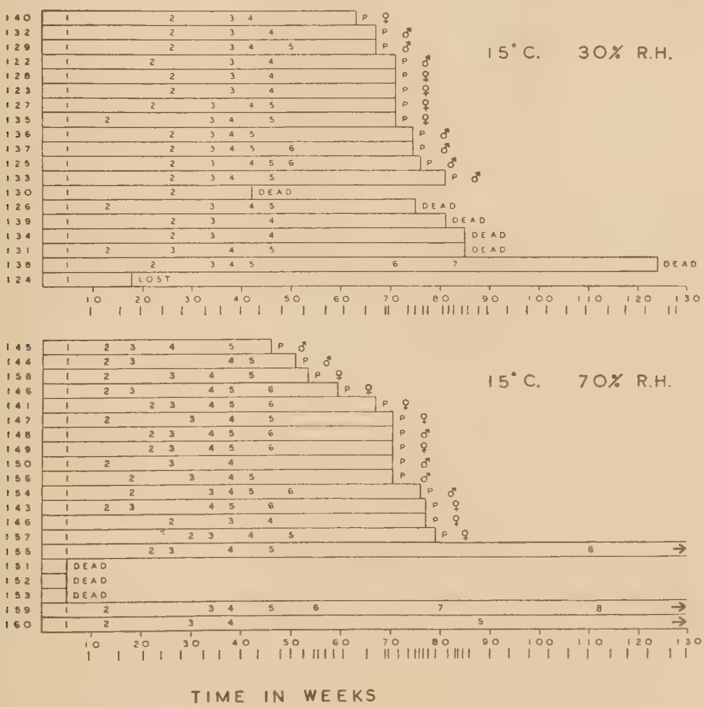

Fig. 5.—Larval development in constant conditions, showing the rhythm of moulting. No. 155 pupated, without moulting again, at the 140th week. Nos. 159 and 160 died, without moulting again, at the 144th and 186th weeks, respectively. For explanation of symbols, see fig. 2.

pupations occurred and these have been termed the second and third active periods. The first active period, composed of larval moults only, commenced with the newly emerged larvae and ceased when the rate of moulting decreased about the 9th–15th week depending upon the temperature (figs. 5–9). The limits of each of these periods were similar throughout the range of temperature studied.

In the laboratory in constant conditions of 15°C., 30 per cent. R.H. (fig. 5), the larvae maintained a rhythm of development, with alternate moulting and resting periods, similar to that occurring in the field. All but one of the larvae moulted once during the first active period and spent the first resting period in the second instar; the exceptional one reached the third instar during the resting period. They moulted 3–5 times during the second active period and spent the second resting period as fully grown larvae. They all pupated during the third active period (m—m—p).

At 15°C., 70 per cent. R.H. (fig. 5), all except the first four individuals to pupate, which are discussed later, developed in a similar manner to those at

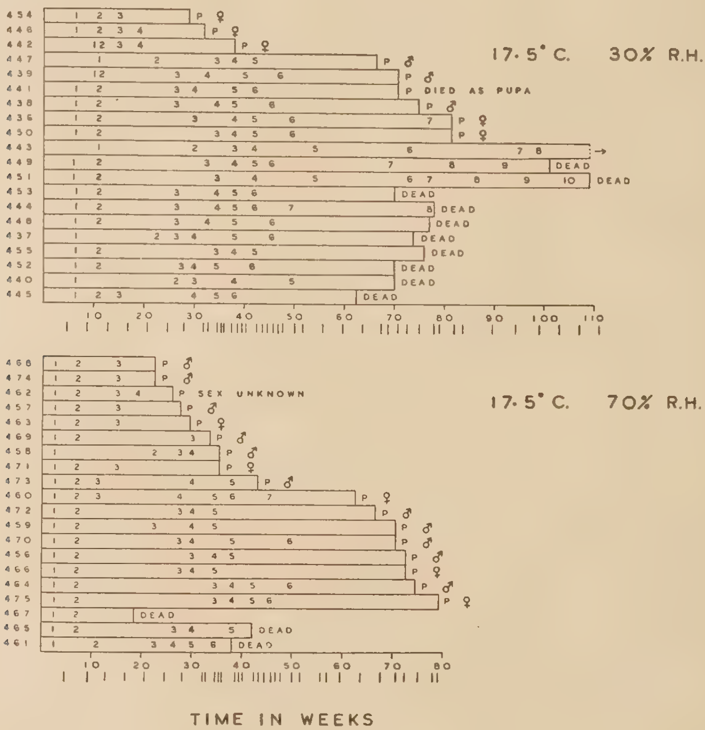

Fig. 6.—Larval development in constant conditions, showing the rhythm of moulting. No. 443 moulted at the 111th and 120th weeks and died at the 127th week. For explanation of symbols, see fig. 2.

30 per cent. R.H. except that more moults occurred during the first resting period. One larva at 70 per cent. R.H. did not pupate until the 140th week and this provides one of the few pieces of evidence for a possible fourth active period.

At 17·5°C., 30 per cent. R.H. (fig. 6), all except the first three, and at 70 per cent. R.H. all except the first nine, individuals to pupate, which are discussed

later, developed with a rhythm similar to that which occurred at 15°C., 30 per cent. R.H., the difference from 15°C., 30 per cent. R.H., being that most moulted twice during the first active period, which was also extended slightly.

At 20°C., 30, 70 and 90 per cent. R.H. (fig. 7), only six individuals (nos. 193, 187, 211, 216, 219 & 239) developed with a rhythm similar to that which occurred at 15°C., 30 per cent. R.H. The remainder are discussed later. The difference from 15°C., 30 per cent. R.H., was that 2–4 moults occurred during the first active period, which was extended as at 17·5°C., and more moults occurred during the first resting period.

Fig. 7.—Larval development in constant conditions, showing the rhythm of moulting. No. 190 moulted at the 136th week and died at the 151st week. No. 181 moulted at the 136th week and died at the 157th week. For explanation of symbols, see fig. 2.

At 22·5°C. and 25°C. (figs. 8 & 9), none of the larvae developed as at 15°C., 30 per cent. R.H.

It can be seen, therefore, that the proportion of pupations that occurred during the third active period decreased as the developmental temperature increased from 15 to 22·5°C., whilst the proportion of pupations occurring during

the second active period increased as the developmental temperature increased from 15 to 22·5°C. (fig. 4).

The rhythm of development for individuals pupating during the second active period is clearest at 20°C. At this temperature the larvae moulted 3–5 times during the first active period, spent the first resting period in the fully grown stage, and pupated during the second active period (m—p).

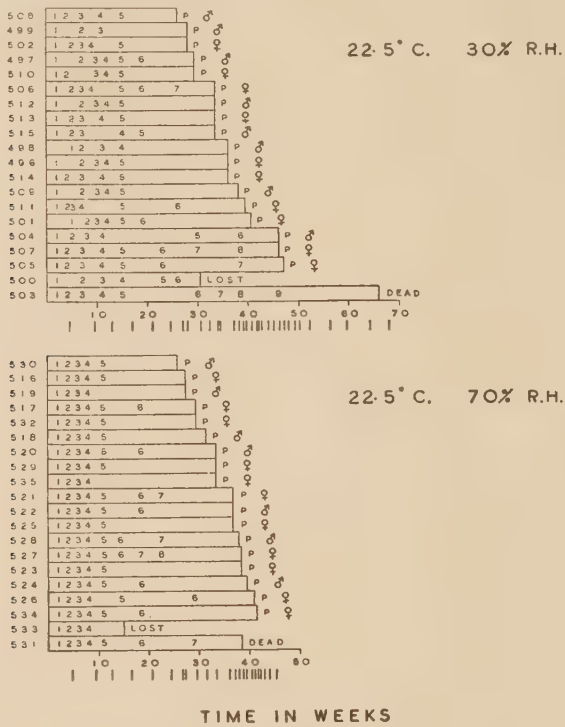

Fig. 8.—Larval development in constant conditions, showing the rhythm of moulting. For explanation of symbols, see fig. 2.

At 22·5 and 25°C. (figs. 8 & 9), the larvae moulted five or six times during the first active period and most moulted at least once during the first resting period, which was spent in the fully grown stage. All pupated during the second active period (m—p).

The rhythms of development of the larvae that pupated during the second active period at 17·5°C. and during the second resting period at 15°C. differed from the rhythms discussed so far in the following ways.

At 17·5°C., 30 per cent. R.H. (fig. 6), the three larvae (nos. 454, 446 & 442) that pupated in the second active period extended their first active period into the 15th to 19th weeks. They then rested for 13, 14 and 19 weeks, respectively, and pupated about the middle of the second active period.

At 17·5°C., 70 per cent. R.H. (fig. 6), six individuals (nos. 468, 474, 462, 457, 463 & 471) developed as above and continued moulting until the 15th–19th week, but then rested on the whole for rather shorter periods; 3 rested for only 7 weeks, 1 for 12, 1 for 14 and one for 20 weeks. The remaining three larvae, which

pupated during the second active period (nos. 469, 458 & 473), maintained the first part of the rhythm of those pupating in the third active period; *i.e.*, they moulted 1–3 times during the first active period, rested during the first resting period, continued their development and moulted 1–3 times during the second active period to reach the fully grown stage. They then pupated at the end of the second active period, without an intervening resting period (m—mp).

At 15°C., 70 per cent. R.H. (fig. 5), the four individuals that pupated before the third active period (nos. 145, 144, 158 & 146) maintained the first part of the rhythm of those individuals that pupated during the third active period. The

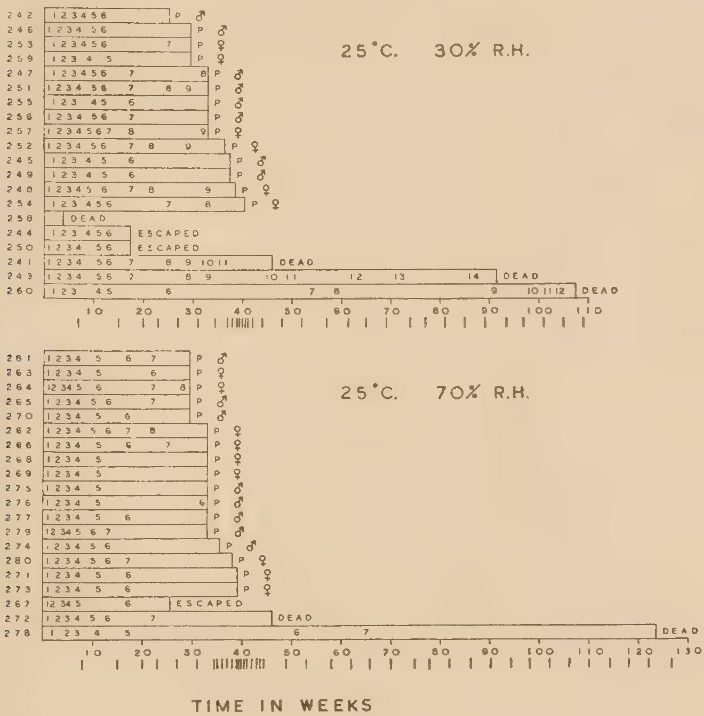

Fig. 9.—Larval development in constant conditions, showing the rhythm of moulting. For explanation of symbols, see fig. 2.

main difference was they did not rest as fully grown larvae for the same length of time as the others; one individual (no. 145) rested, as a fully grown larva, for so short a period, if at all, that it pupated at the end of the second active period (m—mp), while the other three (nos. 144, 158 & 146) rested for longer periods and pupated one after the other throughout the second resting period. This development may be compared with the development of nos. 469, 458 and 473 at 17·5°C., 70 per cent. R.H. (fig. 6), in which the larvae rested in an early instar and then during the second active period completed their development and pupated apparently without an intervening resting period (m—mp).

Summarising then, larvae that pupated during the third active period rested twice in their development; once during the first resting period, mainly in an early instar, and again during the second resting period as fully grown larvae (m—m—p). The larvae that pupated during the second active period rested

once, either in an early instar or as fully grown larvae, giving the developmental patterns of m—mp or m—p, respectively.

At 17·5°C., there was a distinct size difference between the larvae which was most marked about the end of the first resting period. Those about to pupate were of the same size as normal fully grown larvae (5 mm.), whilst those that had been inactive during the first resting period were of a size appropriate to about the third instar (3 mm.). This size difference was not observed at 15 or 20°C.

The experiments at 15, 20 and 25°C. were started about the 30th July 1951, whilst those at 17·5 and 22·5°C. were started about the 30th November 1952. The larvae developing in controlled alternating conditions (see below) and in constant conditions with malnutrition (p. 764) were set up on the 6th November and the 6th December 1951, respectively, and were the progeny of adults from the cultures. Thus, although the month of starting development varied from August

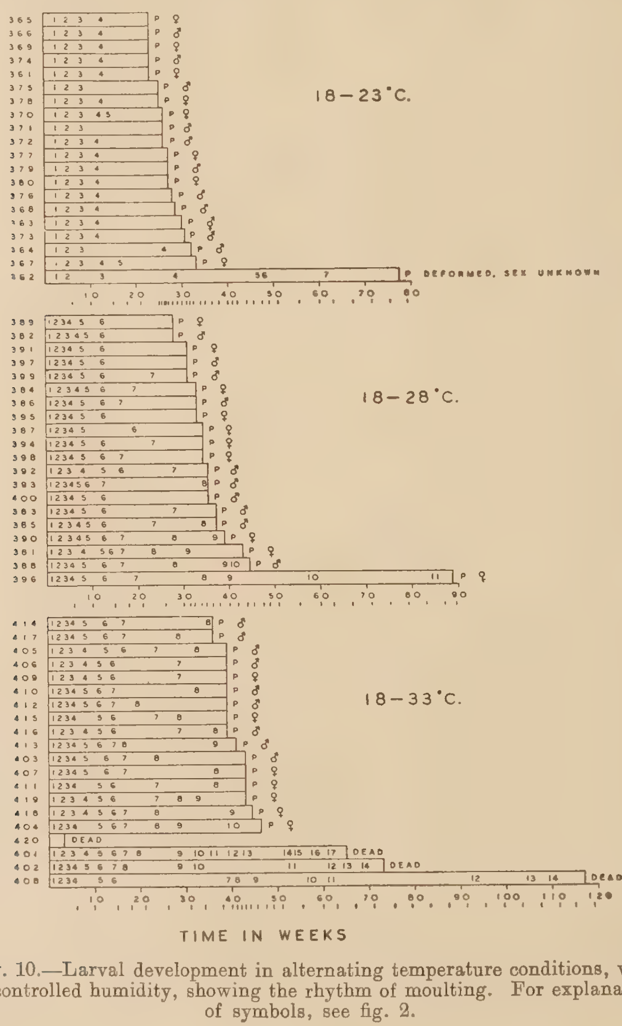

Fig. 10.—Larval development in alternating temperature conditions, with uncontrolled humidity, showing the rhythm of moulting. For explanation of symbols, see fig. 2.

to December, all the larvae followed the same temporal rhythm and pupated during the active periods (fig. 4).

The effects of 30 and 70 per cent. R.H. on the larval development were similar except at 15 and 17·5°C., where the higher humidity seemed to favour earlier emergence. At 90 per cent. R.H. the food became caked by moulds and all the larvae, except three at 20°C., died during the first three months.

Larval development in conditions of controlled alternating temperatures.

With alternate 12-hr. periods (see p. 754) at 18 and at 23°C., the mean temperature experienced was 20·5°C. The larvae that developed in these conditions (fig. 10) showed a pattern of development similar to that of most larvae kept at a constant temperature of 20°C. (m—p).

When the temperature alternated between 18 and 28°C. (fig. 10), the mean temperature experienced was 23°C. and the larvae showed a pattern of moulting similar to that of larvae kept at the constant temperatures of 22·5 or 25°C. (m—p). However, one larva pupated successfully at 88 weeks in the third active period (m—m—p). This individual, together with two that developed in constant conditions with malnutrition (p. 765) and three in the preliminary experiments at 25°C. (below), were the only ones, at mean or constant temperatures of 22·5°C. or above, to pupate successfully as late as the third active period.

When the temperature alternated between 18 and 33°C. (fig. 10), the mean temperature experienced was 25·5°C., but the time spent at the unfavourably high temperature of 33°C. either caused an increase in the length of the resting period or delayed the onset of pupation.

In general, the rhythm of development in alternating-temperature conditions was similar to that which occurred in constant conditions at a temperature equal to that of the mean.

Larval development in extreme conditions of temperature.

Low temperatures.—At 5°C., 30, 70 and 90 per cent. R.H., none of the larvae moulted and all had died by the 20th week. At 10°C., 30 and 90 per cent. R.H., none moulted and all had died by the 28th and 35th weeks, respectively, but, at 70 per cent. R.H., four individuals moulted and grew very slowly. One of these survived for six months, two for nearly three years, whilst the fourth had moulted five times and was still living after three and a half years. None pupated.

High temperatures.—The effects of high temperature on the developmental period were studied, by means of observations on times of pupation, in a preliminary experiment not previously mentioned. Cultures, set up with adults collected in the field, were kept at 25°C., 70 per cent. R.H., and when the larvae were about 14 weeks old, 20, in individual tubes, were placed under each of the following conditions:— 20, 25, 30, 35 and 40°C. at 30, 70 and 90 per cent. R.H. for each temperature. The food given to each larva consisted of a whole dried *Lucilia* larva, a small quantity of debittered yeast and a piece of wool treated with cholesterol and yeast (see p. 752).

The results showed that under each set of conditions there were two groups of larvae, which pupated at widely different times. At 20°C., 30, 70 and 90 per cent. R.H., a total of 30 larvae pupated, 23 at about 35 weeks, and 7 between 74 and 96 weeks. At 25°C., a total of 22 larvae pupated, 19 at about 39 weeks, and 3 between 74 and 96 weeks. At 30°C., one pupated at about 30 weeks but it died in the pupal stage. At 35 and 40°C., none pupated. These larval periods include the 14 weeks spent in the cultures at 25°C. 70 per cent. R.H., during which time the larvae reached the fully grown stage. The times of pupation in this experiment confirm the presence of the second and third active periods seen in the main experiment but they are not included in any of the figures.

Of the constant temperatures studied, the highest at which larval development was completed satisfactorily was 25°C., and therefore the maximum temperature for successful larval development lies between 25 and 30°C.

Larval development in conditions of constant temperature and humidity with malnutrition.

This experiment was designed to show the rate of development, more accurately than was possible in the previous experiments, of five larvae in each of the following conditions: 15, 20 and 25°C., with 70 per cent. R.H.

The diet was restricted to a small portion of wool treated with cholesterol and yeast (p. 752) to enable the weekly observations to be made more rapidly and more accurately. Cast skins were removed and their overall length measured under the microscope using a micrometer eyepiece.

The data indicate that the larvae suffered malnutrition, compared with individuals kept in the same conditions of temperature and humidity in the previous controlled-temperature experiments, because larval mortality was greater, the rate of development was slower and the pupae formed were smaller.

Eleven out of the 15 larvae died but the other four pupated successfully (fig. 11).

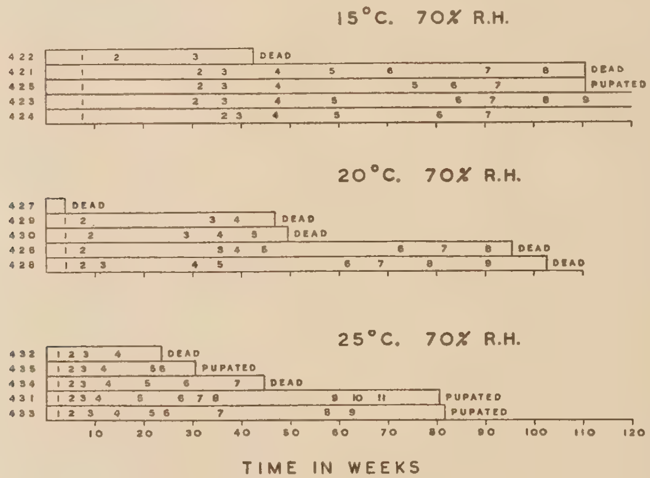

Fig. 11.—Larval development in constant conditions of temperature and humidity with malnutrition, showing the rhythm of moulting for individuals. Observations were made weekly, the moults are numbered, and time of pupation or death is shown.

The rhythm of development was similar to that occurring in the previous experiments (pp. 757–762), but the speed of development was slower, so that the larvae tended to pupate in a later active period.

At 15°C., no. 425 (fig. 11) was an excellent example of rhythmic development; moulting once in the first active period, three times in the second active period, three times in the third active period and finally pupating in the fourth active period at 111 weeks, *i.e.*, m—m—m—p.

At 20°C. (fig. 11), the larvae moulted with a rhythm similar to that occurring at 15 or 17·5°C. in the previous experiments (p. 758), but none pupated successfully.

At 25°C. (fig. 11), the rhythm of development of no. 435 consisted of moulting during an extended first active period followed by a short resting period and then

moulting and pupating (at 31 weeks) during the second active period, *i.e.*, m—mp. The rhythms of nos. 431 and 433 consisted of continuous moulting up to the end of the second active period, although there was a slight decrease in the rate during the first resting period, followed by complete rest during the second resting period and then further moulting and pupation (at 81 and 82 weeks) during the third active period, *i.e.*, m—m—mp.

Larvae in the previous controlled-temperature experiments pupated when about 5 mm. in length, whilst the lengths of the skins in which the larvae pupated in this experiment ranged from only 3·4–4·4 mm.

Effect of temperature on the number of moults.

The number of larval moults depends upon the temperature and the time spent as a larva; the effects of relative humidities of 30 and 70 per cent. are not appreciably different. For any given temperature, larvae that pupate in the third or fourth active period undergo more moults than those that pupate in the second active period. The number of larval moults increases with rise in temperature both for larvae that pupate in the second active period (Table II, 17·5–20°C.),

TABLE II.

Frequency distribution of numbers of larval moults showing an increase in the numbers with rise in temperature.

Temp. (°C.)	Active period in which pupation occurred	No. of individuals	Number of larval moults								
			4	5	6	7	8	9	10	11	12
15·0	3rd	26		7	11	8					
	4th	2				2					
17·5	2nd	12	7	4	1						
	3rd	14			5	7	2				
20·0	2nd	31	2	19	9	1					
	3rd	6				1	3	2			
22·5	2nd	36	1	3	16	10	4	2			
25·0	2nd	31			4	12	7	4	4		
18–23	2nd	19	2	14	3						
	3rd	1					1				
18–28	2nd	18				7	7	1	2	1	
	3rd	1									1
18–33	2nd	16					2	10	3	1	

and for those that pupate in the third active period (Table II, 15–20°C.). The effect of temperature on the number of moults is very marked in the alternating conditions shown in fig. 10. At 18–23°C. (mean 20·5°C.), the number of moults was similar to that recorded for the constant temperature of 20°C., but at 18–28°C. (mean 23°C.) and 18–33°C. (mean 25·5°C.), the effect of the high temperatures of 28 and 33°C. can be seen in the increased number of moults compared with the number recorded for the constant temperatures of 22·5 and 25°C. The fact that high temperature increases the number of moults is

confirmed in the preliminary experiments which were started with fully grown larvae and in which an excessive number of extra moults occurred at both 30 and 35°C. The rate of extra moulting, approximately one moult per month, was similar for 30 and 35°C., but the larvae survived longer at 30°C. and therefore underwent more moults (Table III). At 35°C., 30 per cent. R.H., 13 out of 20, and, at 70 per cent. R.H., one out of 20 larvae became markedly smaller in size, decreasing from about 5 mm. (the length when first put to 35°C.) to 2 mm.

TABLE III.

Frequency distribution of numbers of extra moults that occurred when fully grown larvae (14 weeks old) were moved from 25°C. to 30°C. and 35°C.

Temp. (°C.)	No. of individuals	Number of moults after fully grown stage reached															
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	19
30	40	1	2	4	2	1	6	1	2	2	2	3	4	5	0	4	1
35	40	2	4	8	0	5	3	3	5	4	1	2	2	1			

Pupal Period.

The effect of temperature and relative humidity on the pupal period was studied. Fully grown larvae were taken from the cultures, supplied with food and examined daily until pupation commenced. The experiment was performed at 10, 15, 20, 25 and 30°C., and 30, 70 and 90 per cent. R.H. for each temperature.

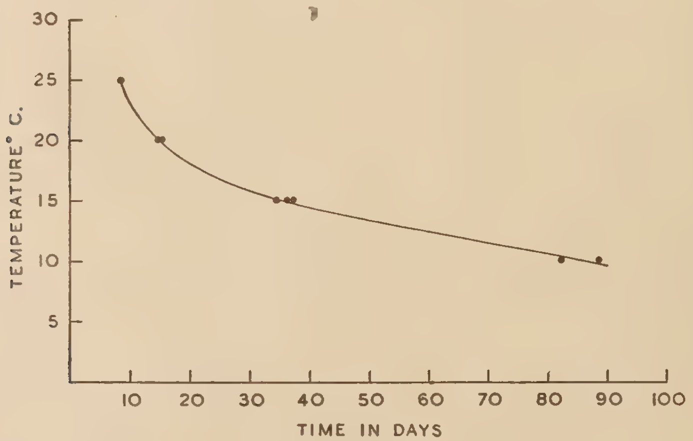

Fig. 12.—Effect of temperature on the length of the pupal period.

It was found that the duration of the pupal period decreased with rise in temperature (fig. 12), but relative humidity had little effect. Successful pupation occurred at 10, 15, 20 and 25°C., but none of the larvae pupated at 30°C. The length of the pupal period ranged from 89 days at 10°C., 90 per cent. R.H. to 9 days at 25°C., 30, 70 or 90 per cent. R.H. At 10°C., pupation was completed successfully at the higher humidities of 70 and 90 per cent. R.H. but at 30 per

cent. R.H. there was a high larval and pupal mortality. Thus, although complete larval development at 10°C. was not possible (p. 763), fully grown larvae placed at this temperature were able to pupate.

At 10°C., 90 per cent. R.H., one individual, which is excluded from the mean figure for 10°C., 90 per cent. R.H. in Table IV, took 24 weeks to complete its pupal development.

TABLE IV.

Effect of temperature and relative humidity on the length of the pupal period.

Temp. (°C.)	R.H. (%)	No. of individuals	Mean pupal period (days)	Range (days)	Mortality (%)		% escaped through muslin
					Larvae	Pupae	
10	30	10	—	—	40	60	—
	70	10	82·1	70–104	0	20	—
	90	10	88·6	70–97	0	20	—
15	30	20	34·6	30–38	5	5	—
	70	20	36·2	28–43	0	0	—
	90	20	37·2	33–41	0	5	—
20	30	20	14·6	11–16	10	0	5
	70	20	15·3	12–19	5	5	—
	90	20	14·6	12–16	0	0	5
25	30	10	8·7	7–10	30	10	—
	70	10	8·5	7–10	20	20	—
	90	10	8·6	7–10	30	0	—

Emergence of Wild Populations.

In October 1952, a total of 689 larvae was collected from a house-sparrow's nest in the eaves of a house, from two dead sparrows and from some woollen material in the attic. There were approximately equal numbers of larvae of sizes corresponding to the 2nd, 3rd, 4th, 5th and 6th instars. Half of each size group was placed in each of the attics of two houses in the grounds of the laboratory. The larvae were given an adequate amount of culture medium and also a little of the natural food (nest material). Thermohygrograph records were kept of these places. The mean weekly temperatures, in the attic that was tiled and boarded internally, were consistently higher than in the other attic, which was merely tiled. The mean attic temperatures for the period October 1952 to May 1954 were 16·3°C. and 14°C., respectively. Observations of pupation and emergence were made during the late winter and early spring.

Pupations occurred during the springs of 1953 and 1954. In both attics, about 80 per cent. of the larvae that were of a size equivalent to 4th–6th instar in 1952 pupated in 1953, but the remainder did not pupate until 1954. All the larvae that were of a size equivalent to 2nd or 3rd instar in 1952 pupated in 1954.

In the warmer loft, although a few pupations occurred before 6th January, the main peak was during February, with the result that adults emerged mainly during March. In the cooler loft, pupations occurred mainly during late March, producing a peak of adult emergence in May.

Similarly, two different times of emergence were observed when adult beetles were collected, both from inside houses and from flowers in the grounds, during the early spring and summer of 1950. Adults were found indoors, on windows, window-sills, white papers and in other similar and well illuminated places, from

early March until the end of July. The numbers collected reached a peak during March and another during May (fig. 13). The peak during March was almost entirely due to collections from rooms in the house possessing the warmer of the two lofts mentioned above. The later indoor peak in May was due to collections from a private house, and the source of these adults was a bird's nest built in the cavity wall.

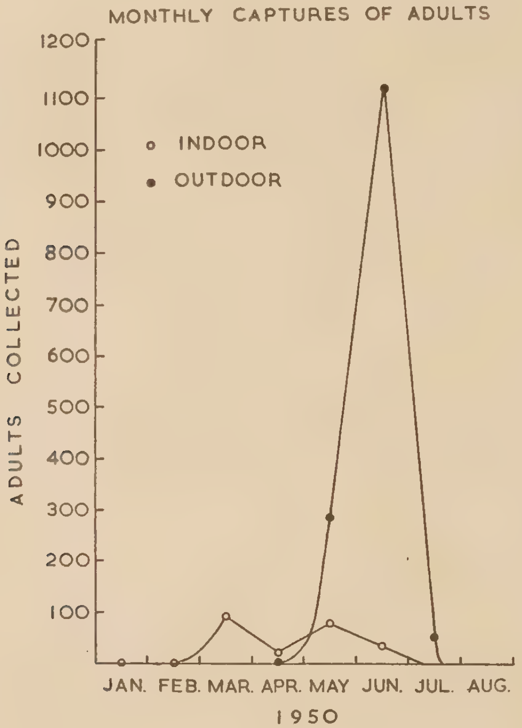

Fig. 13.—Monthly collections of adult beetles during 1950; outdoor captures from flowers, indoor captures mainly from the inside of windows.

Adults were collected from flowers in the grounds from the end of April to the end of July, and the numbers reached a peak during June (fig. 13). Although the outdoor collections were subject to prevailing weather conditions, collections were made on most days during May, June and July except for a cold spell at the end of June and the beginning of July.

These results indicate that the time of emergence is closely correlated with the mean temperature, and that under normal field conditions, and with the food naturally available, most of the larvae require two or more years in which to complete their development.

Discussion.

Given food of high quality, as used in the cultures, *Anthrenus verbasci* has a two-year life-cycle under outdoor fluctuating conditions in southern England. Active development of all stages takes place during the summer months but there is a cessation of growth during the winter, which is spent as a resting larva.

Larval development extends over two summer seasons, so that the first winter is spent as a young larva and the second as a fully grown larva. Pupation takes place in the spring. This cycle of active growth followed by rest is synchronised with the seasons and constitutes an annual rhythm of development. A most remarkable feature of the development of this species is that this cycle of active growth and rest persists when development takes place under constant physical conditions in the laboratory. The mechanism of the regulation of this rhythm of development has not as yet been determined.

Dormancy in insects has received increasing attention in recent years and the subject has been reviewed in detail by Lees (1955). There are two main types of dormancy. The simpler is termed quiescence and is characterised by a cessation of activity during exposure to unfavourable conditions. This is simply an immediate and direct response to an unfavourable environment. But in many insects, the dormant condition is a more complex physiological state, termed diapause. The onset of diapause, in most instances, occurs well in advance of the adverse conditions it serves to withstand. The factors controlling the onset differ from species to species, but virtually all so far discovered have been environmental signals indicative of the passing seasons; for example, length of day, rate of change in length of day, temperature, leaf senescence. However, although simple seasonal signals for the onset of diapause are of obvious value to multivoltine species with a facultative diapause, this is not so for univoltine and semivoltine species with an obligatory diapause (*i.e.*, every individual of each generation enters diapause). And, in fact, most species that possess an obligatory diapause behave as if they were insensitive to the environment, that is, they enter diapause irrespective of the external conditions.

Larvae of *A. verbasci* have been bred in the laboratory under a range of developmental temperatures, extending both above and below the optimum, but all without exception have passed through a dormant period. The shortest larval development time was 22 weeks at 20°C. There seems little doubt that these dormant periods may be regarded as periods of diapause and that the diapause is an obligatory one.

No obvious external changes occurred when larvae entered diapause, and therefore in these experiments the stated limits of diapause are only approximate. The cycle of active development followed by diapause, which occurred under constant conditions in the laboratory, may be described as follows.

A period of active development followed immediately on emergence from the egg. During this period, when larvae were actively growing and showing an observable increase in size, there was a high rate of moulting, but after about 12 weeks, perhaps slightly less at lower temperatures, a sudden fall in the rate of moulting took place; in fact nearly all individuals virtually ceased to moult. It is assumed that the onset of diapause occurred shortly after this sudden fall in the rate of moulting. During this first active period, the growth or increase in size that took place was roughly proportional to the temperature; so that those larvae that were developing at low temperatures were only about half-grown at the onset of diapause, whilst those developing at higher temperatures, were fully grown. The first signs of renewed activity after the first diapause were the pupation of the fully grown larvae (m—p), and the recommencement of growth and moulting by the smaller larvae, which during this second active period reached the fully grown stage. For these fully grown larvae there now followed a second diapause, on completion of which the larvae pupated, thus signalling the beginning of the third active period and completing the equivalent of a two-year life-cycle (m—m—p).

A striking aspect of the life-cycle is the frequency distribution of pupations which, for larval development at a series of constant conditions, is clearly bi-modal (fig. 4). The significance of this observation is greatly increased by the fact that

the second active period of moulting for the small larvae (*i.e.*, those developing with a two-year life-cycle) occurred at the same time as the first peak of pupation for those developing with a one-year life-cycle. This alignment of active periods, between individuals developing at different temperatures, and therefore at different stages in their development, indicates a basic rhythm of development within the species.

The length of the cycle in this rhythmic development under constant conditions is about 41 weeks compared with the annual rhythm of development under outdoor fluctuating conditions. It appears at first sight that the rhythm is modified under constant conditions, but facts described below suggest that the shorter interval may represent the basic periodicity.

The times of pupation of larvae in a series of fluctuating conditions of increasing mean temperature were as follows. In the screen and summer-house, 1st May; in the storage hut, the middle of March; in the cooler of the two lofts, during March; in the warmer of the two lofts, during February. A similar hastening of pupation has been recorded by Waloff (1949) for *Ephestia elutella* (Hb.). In this country, *E. elutella* spends the winter in a resting stage and, in unheated warehouses, it pupates in April and May. Waloff collected larvae from the field during the winter and placed them at 25°C., and found that " by January the larvae at outdoor temperatures reach a certain physiological state in which pupation is delayed not by the original diapause inducing factors, but by the low outdoor temperatures which delay immediate pupation ". Similarly, Kuwana (1951) found that if the larvae of *A. verbasci* are transferred during February from natural conditions to 25°C. they pupate within a few days, although they do not do so if such a transference is made during December.

These facts suggest that the shorter interval is the basic one and that when diapause is completed, activity (involving both moulting and pupation) will proceed forthwith if the temperature is above the threshold for development. This also furnishes an explanation for the lack of variation in the time of pupation in the screen and summer-house compared with constant or alternating conditions. It is considered that the variation lies in the time of cessation of diapause, so that under outdoor conditions all larvae will have completed their diapause before the temperature rises above the threshold for development, and in the spring, when this threshold is reached, all will be ready to pupate. Under the constant- and alternating-temperature conditions studied—all above this threshold—pupation followed immediately on the termination of diapause, resulting in a wide range of times of pupation.

Factors in the external environment which might be responsible for maintaining rhythmic development under apparently constant conditions were examined in detail. Any possible controlling factor associated with the seasons, including slight seasonal temperature fluctuations in the constant-temperature rooms, were ruled out by the fact that the experiments were not all started at the same time of the year; some commenced in August, some in November and some in December. Relative humidity was controlled within the desiccators and so far as is known it remained constant.

The lengths of the light and dark phases have been shown to be responsible for controlling the onset of diapause in many species of insects, and it is of frequent occurrence that diapause is absent or partially absent when an insect is reared either in continuous illumination or in continuous darkness. According to Lees (1955), Danilevskiĭ & Glinyanaya (1950) suggest that the mechanism controlling the arrest of diapause in insects cannot function when a rhythmical alternation of light and darkness is lacking. However, the present experiments were carried out in complete darkness, except for short exposures of the insects to daylight when they were being examined and to tungsten illumination during visits to the constant-temperature rooms. Uncompleted experiments strongly suggest that the

rhythm of development is unaffected by light regimes of 8 and 12 hours light in a 24-hour cycle.

Starvation may induce diapause in some insects (Lees, 1955). The effects of malnutrition are shown in the experiment on p. 764; although the development was slower under these conditions, the larvae maintained the rhythm by dropping one phase behind, so that at 25°C. the larvae developed with the equivalent of a two-year cycle (fig. 4A), compared with a one-year cycle for larvae fed on a balanced diet (fig. 4C). This does not suggest that starvation is a controlling factor for the onset of diapause.

Neither does it appear that the rhythm is much affected by the physical conditions experienced by the parents. Some experiments (17·5°C., 22·5°C. and alternating conditions) were started with the progeny of adults from the cultures, whilst others (5, 10, 15, 20 and 25°C.) were started with the progeny of adults from flowers and all the eggs were incubated at 20°C., 70 per cent. R.H.

Griswold (1941), working on *A. verbasci* in America, observed the larval development at room temperature of 47 individuals, of which 45 took between 32 and 46 weeks and two took 86 and 90 weeks to complete their development. These results agree with those obtained in the present study and support the conclusion that they are not greatly dependent upon local conditions.

One simple explanation, for the presence of both one-year and two-year cycles in the life-history, would be the existence of two strains within the same species with different developmental periods. To examine this possibility more closely the following breeding experiment was carried out.

The five adults that developed with a two-year cycle and that emerged between the 71st and 75th weeks in the life-history experiment at 20°C. (fig. 7), were allowed to interbreed, and 22 viable eggs were produced. These were incubated, and the larvae allowed to develop at 20°C., 70 per cent. R.H. under the same conditions as for the life-history experiment (p. 753). Of the 20 larvae that successfully completed development, 18 pupated after from 24–33 weeks (*i.e.*, with a one-year cycle) and two pupated after 79 weeks (*i.e.*, with a two-year cycle). Two larvae died, one at 56 and the other at 58 weeks.

If, in fact, there were two strains of *A. verbasci*, then the progeny of the cross described above should include a high proportion of individuals taking two years to develop. In fact, the proportion of two-year cycles was only 10 per cent. and was similar to that obtained in the life-history experiment at 20°C. This shows fairly clearly that the two lengths of life-cycle are not merely characteristics of the progeny of two separate strains of *A. verbasci*.

One of the more striking features of the regulation of the life-cycle in this species is the fact that the active periods in the larval development coincided, roughly, throughout the range of conditions studied. Since all the larvae were 0–1 days old at the start of the experiment, it is evident that the rhythm is a function of age.

However, within certain restricted limits, the rhythm appeared to be modified by temperature. For example, at low constant temperatures there was a tendency for the first diapause to set in a little earlier than at the higher constant temperatures (*cf.*, fig. 5 and fig. 6). Also, at temperatures of 20°C. and upwards, pupation appeared to be delayed (or diapause extended) as the temperature increased. This tendency was most marked in the alternating-temperature experiment (fig. 4B).

At the intermediate temperature of 17·5°C. (fig. 4C), about half the larvae followed the rhythm of a one-year cycle (m—p) and half that of a two-year cycle (m—m—p). There were also individuals which at this temperature seemed to follow the first part of a two-year cycle, but which pupated immediately after the fully grown stage was reached, so that development was completed in one year (m—mp) (fig. 6, nos. 469, 458 & 473).

At 15°C., 70 per cent. R.H., there was another example of this (fig. 5, no. 145), and three examples of an incomplete two-year cycle (nos. 144, 158 & 146), in which pupation occurred during what, for most specimens, was the final diapause period. There is some similarity between these two types of development. In the first case, diapause of the fully grown larva was either absent or very short so that pupation occurred during the second active period, whilst, in the second case, diapause was present although of less than normal duration, so that pupation occurred during what for other specimens was the diapause period. The fact that the only departures from the general rhythmic pattern (3 individuals out of a total of 217) occurred at 15°C., 70 per cent. R.H. suggests that a low mean temperature may be unfavourable to the successful regulation of development.

It is possible that the rhythmical onset of diapause may be hormonally controlled. Wigglesworth (1954) states that " development in the insect is controlled by the changing balance between the growth and moulting hormone, which initiates growth and favours the differentiation of imaginal structures and the juvenile hormone which favours the differentiation of larval structures. Metamorphosis results from a relative decrease in the activity of the juvenile hormone." As early as 1934, Wigglesworth suggested that insect diapause might be due to a temporary failure in the secretion of the moulting hormone. Moulting, in *A. verbasci*, has been shown to be rhythmic and under conditions of malnutrition it was not always accompanied by growth, which suggests that production of the moulting hormone may itself be rhythmic, and not necessarily related to growth. If this can be shown, then the immediate onset of diapause may be due to a shortage of thoracic-gland hormone.

It has been shown by Harker (1956) that the diurnal rhythm of activity of *Periplaneta americana* (L.) is regulated by a secretion from the sub-oesophageal ganglia. If annual rhythms are also hormonally controlled, that of *A. verbasci* may be explicable in terms of an endocrine centre (possibly the sub-oesophageal ganglia) secreting at appropriate intervals a hormone which inhibits the production of thoracic-gland hormone by acting on the gland either directly or *via* the brain, and so inducing diapause. Besides being entirely speculative at present, this hypothesis simply pushes back one step the problem of how to account for the existence of an internal " clock " largely independent of variations in external conditions.

Readio (1931) observed that *Reduvius personatus* (L.) apparently ceased development during the winter months even though kept at room conditions with adequate food. Adult bugs may be found in Kansas from May to September and the eggs take about 20 days to hatch. In the autumn, representatives of all five nymphal instars may be present, and by the middle of November all will have entered dormancy irrespective of the stage of development. If nymphs are reared at room temperature, development is completed during the following spring. Readio moved nymphs of all stages and at various times during the dormant period to 27°C. or above and found that he could thereby stimulate moulting in nymphs up to the fourth instar, but not in fifth-stage nymphs. He concluded that dormancy was progressively more intense in the later stages of nymphal development.

If Readio's results are tabulated, it is found that there is a rhythm of development the periodicity of which is very similar to that found in *A. verbasci*. Moulting ceased, for those individuals that he weighed regularly, between the 9th and the 14th weeks, and all the adult emergences, to whatever temperatures the nymphs had been subjected, occurred between the 35th and the 47th weeks. Of the eight individuals that died in the 5th instar, one died at 33 weeks and seven between the 68th and 70th weeks. These periods of activity coincide well with those found in *A. verbasci*. Whether rhythmic development of this pattern based on an annual cycle of activity is widespread among insects remains to be discovered.

Readio's results also show that individuals that are not fully grown by the onset of the first resting period (at 9–14 weeks) may be stimulated by high temperature to continue their development, thus moulting during what would normally be a resting period. Stimulating fifth-instar nymphs by high temperature, however, was not successful in causing premature emergence. This suggests that the rhythm is organised in such a way as to permit continuance of development to the fully grown stage, should external conditions particularly favour it, but, as if to prevent emergence of the adult at the wrong season, the rhythm at this stage in development is not modifiable by external conditions.

Kuwana (1951) studied the development of *A. verbasci* in Japan. From his English summary (on which the following commentary is based), it seems that under natural conditions he found one generation a year. Apparently he did not observe a two-year cycle in this species. However, it is not clear whether his statement was merely a field observation, in which case semi-voltine individuals could have been overlooked, or whether it was the result of a field experiment. Under laboratory conditions he found that the shortest larval development (8 months) occurred at 20°C., whilst, at 15 and 25°C., development took longer, and at 30°C. there was hardly any pupation. This confirms that the range of temperatures over which successful larval development can take place is 15–25°C. However, the shortest larval development period quoted (8 months) is considerably longer than the five months recorded in the present study. A very important point of difference here is that he does not record, for any one temperature, two significantly different developmental periods.

Kuwana found that if larvae are transferred, during February, from natural conditions to 25°C., they pupate within a few days, although they do not do so if such a transference is made during December. He also performed a laboratory experiment in which he transferred larvae (4 months old) from 25°C. to 5–20°C. for 1–4 months, finally returning them to 25°C. Those that had been exposed to 5°C. did not pupate, a few of those at 10–20°C. pupated after three months, and at 15 and 20°C. nearly 100 per cent. pupated after four months. He concluded that " the larvae have a kind of block for pupation, which is similar to diapause, and that for passing over the block, temperatures in a specific range, as shown above, are effective ". These observations do not seem to show that exposure to any particular temperature is necessary before pupation can occur but only that larval development, including diapause, proceeds at different rates at different temperatures within the developmental range.

Diapause is of value to *A. verbasci* because it regulates development and induces a rhythm in the life-cycle which is synchronised with the seasons. Under natural conditions, diapause terminates during the winter, so that in the spring, when the temperature rises, nearly all the fully grown larvae pupate, producing a peak of adult emergence. The effect of temperature on the length of the pupal and inactive adult periods (fig. 12) is such that during a fine warm spell the development time is decreased, resulting in an even closer peak of adult emergence. Peak emergence occurs in June, when the maximum hours of sunshine favour flight and when the flowering season of the plants on which the adults aggregate to feed on the pollen and nectar is at its height. Synchronised emergence is of value to *A. verbasci* for, particularly in an insect whose adult life is relatively short, it greatly increases the chances of mating. This must be of considerable importance in areas where the population is small or thinly dispersed.

Summary.

Anthrenus verbasci (L.) (Col., DERMESTIDAE) is a pest of dried animal materials and is widely distributed in temperate regions.

The effects of temperature and relative humidity on development have been

studied. It is shown that the periods of incubation and pupation decrease with increase of temperature, the former from 54 days at 15°C. to 12 days at 30°C., and the latter from 89 days at 10°C. to 9 days at 25°C. Humidity differences have little effect.

The larval development is exceptional in that under constant physical conditions in the laboratory there is a rhythmical onset of the larval diapause, *i.e.*, development is regulated into one or more cycles, each comprising a period of active growth followed by diapause. The length of this cycle under constant conditions is considerably less than a year. Larval development may extend over one or two cycles depending mainly upon the temperature. At low temperatures of 15°C., development extends over two cycles; at 20°C. and above, only one cycle is needed; at the intermediate temperature of 17·5°C., half the larvae require one and half require two cycles in which to complete their development.

When the larvae developed under constant physical conditions with malnutrition the rhythm of development was maintained, but the larvae tended to require an extra cycle for development compared with those fed on an adequate diet.

Under three sets of controlled alternating temperatures (ranging from 18 to 33°C.) the rhythm of development was similar to that which occurred in constant conditions at a temperature equal to the mean.

The number of larval moults increased both with temperature and the time spent as a larva. At the unfavourably high temperatures of 30 and 35°C., larvae moulted an excessive number of times; one larva at 30°C. moulted 19 times after the fully grown stage was reached; and, at 35°C., 30 per cent. R.H., 13 out of 20 larvae gradually decreased from about 5 mm. (the length when first put to 35°C.) to 2 mm., moulting a number of times in the process.

Under outdoor fluctuating conditions, the resting period in the cycle is extended, due to the winter temperatures prevailing for some time after the end of diapause. Active development commences again in the spring when the temperature rises, and in this way the cycle is synchronised with the seasons into an annual rhythm of development. The life-cycle under outdoor conditions may take one, two or more years to complete.

Field populations, developing both in attics of houses and under more outdoor conditions, pupated from January to May, the time of pupation being mainly dependent upon the ambient temperature prevailing after the termination of diapause.

Diapause is of value to *A. verbasci* because it induces a rhythm in the life-cycle which synchronises with the rhythm of the seasons and ensures that the adults are present when the environment is favourable for their activity, *i.e.*, during May and June when the maximum hours of sunshine favour flight and the preferred flowers are in bloom.

The mechanism by which the rhythmical onset of diapause is controlled has not been investigated.

Acknowledgements.

I am indebted to Mr. G. V. B. Herford, Director of the Pest Infestation Laboratory, for permission to present an account of this work to the University of London as part of a Ph.D. degree thesis, and to Mr. M. E. Solomon and other colleagues of the Biology Section for much helpful discussion and criticism.

Miss R. Borrett has given invaluable assistance with the practical work; the photographs were prepared by Mr. J. H. Hammond and Mrs. A. Price.

This work was undertaken as part of the research programme of the Pest Infestation Laboratory, and is published by permission of the Department of Scientific and Industrial Research.

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0·75 mm. approx.

FIG. 2. Young larvae. Length 1 — 3·5mm. approx.

FIG. 3. Fully grown larva, dorsal view (right) and ventral view (left). Length 5 mm. approx.

/al skin. Length 5 mm.

FIG. 5. Inactive adult in last larval skin. Pupal skin has been pushed backwards.

FIG. 6. Active adult. Length 3·5mm. approx.

STAGES IN THE LIFE-CYCLE OF *ANTHRENUS VERBASCI*.

STUDIES ON THE CHEMICAL CONTROL OF WIREWORMS (*AGRIOTES* SPP.).

II.—THE DIRECT AND RESIDUAL EFFECTS OF BHC, DDT, ALDRIN AND CHLORDANE.

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Potter, Healy & Raw (1956) described two field experiments carried out at Rothamsted from 1947 to 1951 to study the direct and residual effects of BHC, DDT, D-D and ethylene dibromide applied to control wireworms (*Agriotes* spp.) in wheat. BHC was very effective for wireworm control but caused off-flavours in some crops. DDT was slow to take effect but had a strong residual action. The soil fumigants were effective in the year of application but were expensive and required special machinery to apply them.

With the introduction of chlordane and later aldrin, both of which showed promise for wireworm control (Zogg, Horber & Salzmann, 1950, 1951; Günthart, 1950; Roark, 1951; Rawlins, Staples & Davis, 1949; Lange, Carlson & Leach, 1949) there appeared to be the possibility of obtaining effective wireworm control economically and with less risk of flavour changes.

A series of experiments was therefore started to compare BHC with chlordane, aldrin and DDT. The DDT was included because it had shown good residual effects and is cheap and generally shows low phytotoxicity, low toxicity to mammals and is not liable to cause off-flavour.

As no arable field with a sufficiently heavy infestation of wireworms was available, several permanent grass fields at Rothamsted were sampled to find a suitable site. Geescroft field, which had been under grass for about 50 years and which had a total wireworm population of about 2·5 million per acre when sampled in the spring of 1951, was finally chosen. The field was ploughed up on 10th November 1951. The soil was clay with flints.

Treatments and experimental Layout.

The following treatments were applied when the seed was drilled on 1st December 1951.

BHC seed dressing	seed treated at the rate of 2 oz./bushel with a dressing containing 20 per cent. γ isomer.
BHC combine-drilled	3·5 per cent. wireworm dust combine-drilled with the seed at $\frac{1}{2}$ cwt./acre giving 2·0 lb./acre crude BHC $\equiv$ 3·8–4·0 oz. γ isomer per acre.
DDT combine-drilled	5 per cent. DDT dust combine-drilled with the seed at 150 lb./acre giving 7·5 lb./acre technical DDT.
Aldrin combine-drilled	1·78 per cent. aldrin dust combine-drilled with the seed at 200 lb./acre giving 3·56 lb./acre technical aldrin.
Chlordane combine-drilled	5 per cent. chlordane dust combine-drilled with the seed at 100 lb./acre giving 5 lb./acre chlordane.

The experiment was laid out as three randomised blocks of eight plots (one for each treatment and three controls), each plot being 14 × 90 ft. (0·0289 acre). Standard practice was followed when applying the insecticides. In 1951 the plots were drilled with Nord Desprez wheat at 3 bu./acre. In 1952 and 1953 the seed rate was reduced to $2\frac{1}{4}$ bu./acre to emphasise the effect of wireworm attack and treatment effect. Nord Desprez was sown again in 1952 and Cappelle in 1953. Each year a basal dressing of 3 cwt./acre sulphate of ammonia was applied in the spring.

Effect of treatments on yield.

The direct effect of each treatment was assessed by the yield of grain at harvest in 1952 and the residual effect by the yield in 1953 and 1954. The results are given in Table I.

TABLE I.

Direct and residual effects of a single treatment with different insecticides on yield of grain.

Yield of grain (cwt. per acre)

		Seed dressing	Combine-drilled				Standard errors	
	Controls	BHC	BHC	DDT	Aldrin	Chlordane	Controls	Others
1952 ..	31·6	32·9	33·6*	31·7	36·3**	33·7*	0·41	1·24
1953 ..	21·6	22·9	30·2**	26·7*	34·6**	32·9**	0·92	2·76
1954 ..	27·2	29·4	32·9**	29·2	31·0*	29·7*	0·60	1·79

** values which significantly exceed the controls ($P < 0{\cdot}01$)

* values which significantly exceed the controls ($P < 0{\cdot}05$)

In the first year, wireworm damage, judged by inspection of plants during the spring and the yield of the control plots, was slight, although the wireworm population was known to be high. Such slight damage is not uncommon during the first year after old grass, especially when seeding closely follows ploughing up, and has been attributed to the wireworms remaining in the old turf while the crop becomes established (Anon., 1944). Nevertheless, at harvest 1952, significantly greater yields were obtained from the plots treated with BHC, aldrin and chlordane, combine-drilled, than from the control plots. The BHC seed dressing and DDT had no significant effect.

In the following year, when wireworm damage judged by inspection of plants in spring and the yield of the control plots was greater, substantial residual effects were shown by BHC, aldrin and chlordane, combine-drilled. DDT was less effective and BHC seed dressing showed no residual effect.

In the third year, BHC, aldrin and chlordane, combine-drilled, again showed residual effects, and DDT and BHC seed dressing showed none.

Effect on plant growth.

In spring each year, estimates of plant height and density were made. Four samples, each consisting of two adjacent one-ft. lengths of drill, were taken at random from each plot. The number of plants and the height of each were

recorded. To supplement these data, the plots were inspected in early August 1953 and 1954 and scored for plant growth and coverage. The scores are comparable within each year but not between years. The results are given in Table II. In general these results bear out those in Table I. At no time did the plant counts in spring show evidence of significant differences in plant numbers between treated plots and controls. In spring 1952 there was evidence of better growth

TABLE II.

Effect of treatments on plant density and height.

	Controls	Seed dressing	Combine-drilled				Standard errors	
		BHC	BHC	DDT	Aldrin	Chlordane	Controls	Others
	Plant numbers (thousands per acre)							
iv. 1952	978	1108	977	1126	1080	1014	42·3	73·3
v. 1953	799	523	946	734	972	884	79·0	138·0
v. 1954	461	503	563	543	468	398	46·9	81·3
	Plant height (cm.)							
iv. 1952	15·3	15·6	15·0	16·7*	16·0	15·3	0·25	0·42
v. 1953	17·8	16·4	20·6*	18·6	20·3*	20·5*	0·65	1·13
v. 1954	25·6	26·8	27·7	27·7	27·6	26·0	0·57	0·99
	Plant growth and coverage (plot scores)							
viii. 1953	17	18	25	21	29	28		
viii. 1954	20	19	23	19	23	21·5		

* values which significantly exceed those of controls ($P < 0{\cdot}05$).

on the plots treated with DDT. The following year, when substantial residual effects on yield were recorded from the plots previously treated with BHC, aldrin and chlordane, combine-drilled, these plots also showed significantly better plant growth in spring and received the best scores for growth and coverage in August. DDT had given a less marked residual effect on yield, and growth on these plots in spring was not significantly better than on the controls and the score for plant growth and coverage in August was intermediate. In 1954, plant growth in spring on the plots previously treated with BHC, DDT and aldrin, combine-drilled, just failed to be significantly better than on the controls but the plots which showed a residual effect on yield, namely BHC, aldrin and chlordane, combine-drilled, also received the best scores for growth and coverage in August.

Effect on the wireworm population.

The plots were sampled for wireworms in November 1951 before the field was ploughed up. They were re-sampled in September 1952 and September 1953 after the crop was harvested and before autumn ploughing. On the first two occasions, four soil samples, each of 4-in. diameter and 9 in. deep, were taken at random from each plot. By September 1953, the wireworm population on some

of the treated plots was extremely low, and on this occasion eight samples were taken from each plot. The wireworms were extracted by a standard flotation method and were then measured and divided into size groups corresponding approximately to first-, second-, third- and fourth-year larvae.

The wireworm population fell greatly during the first year after ploughing. This fall in population is characteristic of newly ploughed grassland irrespective of the application of insecticides and is due largely to the absence of first-year larvae through reduced oviposition in arable soil. To illustrate this, and to take account of it when examining the effect of the insecticide treatments on the wireworm population, analyses were carried out, first, on all the larvae and then omitting first-year larvae.

For analysis and significance tests the wireworm counts were transformed to square roots. The untransformed data are given in Table III. Standard errors are not applicable to these data, and the asterisks refer to significant differences in the transformed data.

TABLE III.

Effect of the treatments on the wireworm population (mean numbers of wireworms per sq. ft.).

	Controls	Seed dressing	Combine-drilled			
		BHC	BHC	DDT	Aldrin	Chlordane
	All larvae					
xi. 1951	52·8	63·0	49·6	64·9	50·6	65·9
ix. 1952	17·8	21·0	6·7*	5·7*	17·2	8·6*
ix. 1953	12·3	10·0	3·8**	3·3**	1·0**	2·9**
	Omitting 1st-year larvae					
xi. 1951	19·7	21·0	21·0	29·6	18·1	25·8
ix. 1952	16·2	18·1	5·7*	5·7*	16·2	5·7*
ix. 1953	7·8	6·7	1·9**	2·9**	0·5**	1·9**

**, * values significantly less than those of the controls ($P < 0{\cdot}01$; $P < 0{\cdot}05$).

The wireworm counts made in November 1951 serve to show that at the beginning of the experiment the population of the plots was reasonably uniform. By September 1952, the population of the plots treated with BHC, DDT and chlordane, combine-drilled, was significantly lower than the control plots. These three treatments, together with aldrin, had a residual effect on yield at harvest 1953. By September 1953, the population of the plots treated with BHC, DDT, aldrin and chlordane, combine-drilled, was markedly lower than that of the control plots. At harvest 1954, BHC, aldrin and chlordane, combine-drilled, showed a residual effect on yield.

The population of the plots originally treated with BHC seed dressing never differed significantly from that of the control plots. This treatment had no residual effect on yield.

Discussion and Conclusions.

All the treatments except BHC seed dressing and DDT were effective, as measured by yield of grain, in the year of application. Good residual effects were obtained from aldrin and BHC, combine-drilled, followed by chlordane, combine-drilled. DDT, combine-drilled, had a residual effect, but this was less marked than that shown by BHC, aldrin and chlordane, and BHC seed dressing showed no residual effect.

There does not appear to be a satisfactory explanation of the failure of the BHC seed dressing in the first year, but its lack of residual effect is in agreement with the results of the earlier experiments (Potter, Healy & Raw, 1956). The ineffectiveness of the DDT in the first year might be partly due to its slowness of action. Indications of slow action were found in the earlier experiments and have been recorded by other workers (Anon., 1949; Lane & others, 1948). The fact that although, in the second year following treatment, the DDT reduced the numbers of wireworms to an extent similar to that caused by BHC and chlordane and lower than that by aldrin, the yield from the DDT plots was significantly lower than the others may be explained in a number of ways. Materials such as BHC, chlordane and aldrin, by virtue of a fumigant effect, may repel wireworms from the treated layer of soil and protect the plants in this way, while DDT, with little or no fumigant or repellent action, may allow the larvae freer access to the plants. It also seems possible that some protection may occur, due to local uptake of insecticide by the plant, in soils treated with BHC, chlordane and aldrin; this may not occur with DDT. A further possible cause which is suggested by the available evidence is that DDT is relatively more effective against the younger larvae, so that although the numbers of wireworms are about the same in the treated plots the proportion of large larvae is greater in the DDT plots and it is the larger larvae which cause the most damage. The detailed population counts made in September 1952 (not shown in Table III) showed 33 per cent. larvae above 1·5 cm. in the DDT plot samples, 14 per cent. in the BHC plot samples and none in either the aldrin or chlordane plot samples. Some further investigation of the action of DDT on wireworms might be of interest since, as mentioned in the introduction, it is cheap, it is relatively non-toxic to mammals, it does not appear liable to cause off-flavours, it has low phytotoxicity and where it is effective it seems to give lasting protection (Morrison & Crowell, 1953; Stone & Foley, 1954; Woodworth & Lane, 1957). Some workers have found it ineffective under the conditions of their experiments (Post, Munro & Knapp, 1947; Arnason, Fox & Glen, 1948; Blanka, 1950; Begg, 1954; Kulash & Monroe, 1955) but it is possible that more consistently effective results could be obtained if more data on its mode of action in controlling wireworms were available.

At the dosage levels applied, aldrin gave the best results, followed by BHC, combine-drilled, chlordane, DDT and BHC seed dressing in that order. The wireworm counts suggest that aldrin is slow to reduce the population, but unlike DDT it can still protect the crop.

Chlordane, although not as effective as aldrin or BHC, gave good control in these experiments but, judging from the literature, it may not give quite such consistent results as aldrin or BHC, since a number of workers have reported it unsatisfactory under the conditions of their experiments (Post, Munro & Knapp, 1947; Dogger & Lilly, 1949; Lange, Carlson & Leach, 1949; Kulash & Monroe, 1954; Begg, 1954; Griffin & Eden, 1954; Kulash & Monroe, 1955). There is also the possibility of chlordane producing off-flavours (Greenwood & Tice, 1949; Merrill, 1952), although this may not be great.

When the results of this experiment are compared with those of a previous experiment (Potter, Healy & Raw, 1956), an interesting point emerges in relation to the increases in yield from the various treatments. In the 1947 experiment, wireworm attack in the first year was heavy, the control plots were virtually

crop failures (yield 8·9 cwt.) and all the treatments gave much better yields than the controls. Even so, the yields from plots treated with ethylene dibromide injected, BHC broadcast and D-D injected gave significantly better yields than the plots treated with BHC seed dressing (32·1, 30·6 and 28·3 cwt./acre respectively against 24·0 cwt./acre). In the present experiment, wireworm attack in the first year was slight, BHC seed dressing had no effect on yield, but significant increases were obtained from plots treated with BHC, aldrin and chlordane, combine-drilled. Against the heavy attack in a previous experiment and light attack in the present experiment the heavier treatments gave better returns.

Summary.

An experiment on Geescroft field, Rothamsted, from 1951 to 1954, tested the direct and residual effects of BHC, DDT, aldrin and chlordane applied to control wireworms (*Agriotes* spp.) in wheat.

The treatments applied were BHC seed dressing at 2 oz./bushel of a dressing containing 20 per cent. γ isomer of BHC; BHC 3·5 per cent. dust, combine-drilled to give 3·8–4·0 oz. γ isomer per acre; DDT 5 per cent. dust, combine-drilled to give 7·5 lb./acre technical DDT; aldrin 1·78 per cent. dust, combine-drilled to give 3·56 lb./acre technical aldrin, and chlordane 5 per cent. dust, combine-drilled to give 5 lb./acre chlordane.

In the year of application, the first out of old grass, when wireworm attack was slight, the plots treated with BHC, aldrin and chlordane, combine-drilled, gave significantly greater yields than the control plots. In the following year, when wireworm attack was heavier, residual effects on yield were observed on plots initially treated with BHC, DDT, aldrin and chlordane, combine-drilled. In the third year, residual effects on yield were observed on the plots initially treated with BHC, aldrin and chlordane, combine-drilled.

No direct or residual effect of BHC seed dressing was observed.

The residual effects are closely associated with the effect of the treatments on the wireworm population.

The results are compared with those of previous experiments and the increases in yield from the various treatments are discussed briefly.

Acknowledgements.

R. M. Dobson, J. W. Stephenson and J. R. Lofty helped to collect and examine the soil samples. H. V. Garner scored the plots for growth and coverage in 1953 and 1954.

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THE BEHAVIOUR OF LARVAE OF *CULICOIDES CIRCUMSCRIPTUS* KIEFF. (DIPT., CERATOPOGONIDAE) TOWARDS LIGHT STIMULI AS INFLUENCED BY FEEDING, WITH OBSERVATIONS ON THE FEEDING HABITS.

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The larvae of the majority of species of *Culicoides* spend most of their lives burrowing in mud. However, they are also, when the necessity arises, active swimmers, and may occasionally be seen swimming in puddles in the marshes and waterlogged ground which most of them inhabit. In the laboratory they can be kept for long periods in dishes of water.

Painter (1927), referring to *C. furens* (Poey) and *C. phlebotomus* (Will.), and Kettle & Lawson (1952), in their work on the immature stages of British midges, state that the larvae are negatively phototactic. Hull, Dove & Prince (1934) report similar behaviour in the larvae of *C. dovei* Hall. On the other hand, Carter, Ingram & Macfie (1920) state that the larvae of *C. accraensis* C., I. & M. are positively " phototropic " when kept in jars in the laboratory.

The larvae of *C. circumscriptus* Kieff., though inhabitants of salt-marshes, can be successfully maintained and reared in fresh-water conditions. During investigations into their habits it was observed that, after being removed from the mud of their natural habitat and placed in a dish of water, the great majority exhibited a negative phototaxis, while a few were either positively phototactic or did not seem to be attracted one way or the other. When the dish was turned through 180°, the larvae immediately reorientated themselves, those of the photonegative group swimming away from the light source and the photopositive larvae towards it. If they were kept in the dish for a few days it was seen that the number of photopositive larvae had increased while that of the other group had correspondingly decreased, indicating a change in taxis on the part of some larvae from photonegative to photopositive. Again, when the dish was turned through 180°, the larvae of the two groups exchanged their positions.

To test this observation under controlled conditions, 182 larvae, which had been taken out of the mud several days previously, were placed in the centre of a trough of water, as described below, and left for six hours. At the end of that time it was found that 109 larvae (59·9%) had migrated to the illuminated quarter of the trough, 21 larvae (11·5%) had migrated to the quarter farthest from the light, and 52 (28·6%) remained in the middle half. On repeating this procedure with 58 larvae, which had been kept in total darkness for three days beforehand, it was found that a still larger proportion (86·2%) showed a photopositive response.

Technique and General Procedure.

To recover larvae, for use in experiments, from samples of salt-marsh mud, the flotation technique devised by Ladell (1936) was employed with some improvements. The samples were broken up and washed through a 10-mesh sieve with a strong jet of water. The filtrate was then washed through 20-mesh and 100-

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mesh sieves and the material retained in both of these was mixed with a saturated solution of magnesium sulphate.

The treatment with magnesium sulphate of the residue in the 20-mesh sieve may be dispensed with, but it has been found that a large proportion of the larvae in a sample, particularly of the larger instars, may be retained in this sieve, so that, even if accurate numbers are not desired, the extra work entailed is worthwhile.

To treat the residues with magnesium sulphate an apparatus was used which was a modified version of that devised by Fenwick (1940) for the recovery of eelworm cysts from soil. A 1-litre flask (fig. 1) was fitted with a collar or

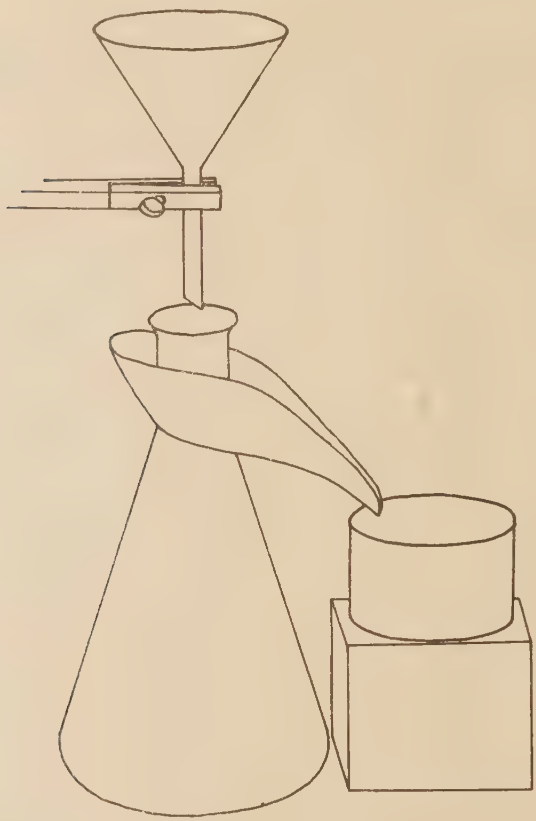


Fig. 1.—The apparatus used for the recovery of larvae from mud samples.

collecting channel moulded with " Vinagel 118 " (Vinatex Ltd.) and hardened by baking in an oven at 160°C. The residue was washed with magnesium sulphate through a funnel into the flask and enough of the solution poured in to reach the top. The sediment was allowed to settle and the larvae and organic débris floated to the top. By pouring in more magnesium sulphate the floating material was washed into the collar and thence into a small glass dish. The sediment was then

stirred thoroughly with a long rod and the procedure repeated once or twice to ensure that all the larvae were obtained. These were then picked from the glass dish by means of a hooked pin and placed in fresh water.

Using this method the larvae are concentrated in a small area and it is much easier to find them and to scoop them out quickly than when the residues are simply mixed with the solution in a dish with a larger surface area.

The culture medium used in some of the experiments described below was that devised by Megahed (1956), consisting of mud rich in organic matter to which a little yeast and charcoal were added. This was put into earthenware pots and covered with water to a depth of ¼ inch and left to " mature " for about three weeks, by which time a rich growth of green algae had usually formed on the surface.

In all the experiments a " Perspex " trough, 24 in. long, 4 in. broad and 2½ in. deep, and marked off lengthwise into quarters, was placed in a darkened room with no source of light other than a 60-watt bench lamp placed a short distance from one end. The end of the trough farthest from the light was painted on the inner side with flat black paint to prevent reflection of the light by the " Perspex ".

The trough was filled with water to a depth of 1 in. and the larvae were introduced at the centre. They were left for one hour, this time having been found sufficient for the majority of them to move to one or the other end of the trough. At the end of this time the larvae from the end quarters of the trough were transferred into the middle of separate troughs and left for another hour. This gave the larvae a second opportunity to orientate themselves and made it possible to discount any which moved in the opposite direction to which they had done before. The great majority of larvae moved to one or other end of the trough and only these have been considered in the experiment. Those which remained in the centre of the trough at the end of each test were ignored. Of these, only a few seemed to be normally active larvae, the rest being dead, moribund, hampered by adhering débris, or, in a few cases, had pupated.

For the sake of convenience and clarity, the experiments and the discussion thereon have been separated into two series. Tests of the type described above were made periodically over a number of days, which varied with each experiment. After each test, all dead or pupated larvae were removed and the remainder, in the earlier experiments of the first series, transferred to a dish of plain tap-water to await the next test.

The larvae used in these experiments were not given food at any time, with the following exceptions. In the middle of some of the experiments the larvae were fed on chopped-up blowfly larvae between tests. This food was chosen since, in eating it, the larvae were still exposed to light. Thus the change in environment imposed by their being given food was limited to that single factor. In order that the ingested blowfly tissue could be seen clearly through the transparent body wall of the midge larvae, they were first vitally stained with Waxolin Red. This fat-soluble stain was sprinkled on the liver on which young blowfly larvae were reared. These eventually became bright pink and on dissection the fat-body was seen to be brightly stained. The other tissues were only slightly coloured but, since a large proportion of the larval tissues consisted of fat-body, it was found that this method gave sufficient indication that the midge larvae had fed.

It was found advisable, in the presence of this type of food, to aerate the water in which the midge larvae were kept between tests, otherwise many of them died. Also, when tests were made subsequent to feeding it was found that many of the larvae were hampered in their movements by adhering pieces of blowfly tissue. This difficulty was partly overcome by putting a thin layer of sand in the dishes, which had the effect of rubbing off some of the material. Before tests were made,

the larvae were carefully extracted from the food with hooked pins and any large adhering shreds of food removed.

In later experiments of the first series, and also in the second series of experiments, midge larvae were kept in a variety of media between tests. To recover the larvae for testing, the medium containing them was simply mixed with magnesium sulphate and the floating larvae picked out with a pin. After testing they were returned to a fresh dish of medium. Since they were required alive and in good condition a water spray was not used to break up the lumps in the medium. Larvae often remained buried in these lumps and, although attempts were made to extract them, many were overlooked. Because of this, as may be seen from the numerical data given in figs. 4, 7 & 8, there were often considerable losses of larvae during the course of the experiments.

Reduction of numbers due to the mortality of the larvae occurred in all experiments, and this generally increased as the experiments progressed. Pupation also accounted for some losses, this being especially marked in fig. 5 where the larvae used were all in the latter part of the fourth instar.

Experiments.

First series.

(*a*) *Details and results.*—In a number of experiments, batches of larvae of *C. circumscriptus* in the third and fourth instar, which had been recovered from the mud 24 hours or less beforehand, were tested periodically, as described above, over different periods of time. The numbers in each batch ranged from 44 to 63 in the case of third-instar larvae, and from 133 to 299 in the case of fourth-instar larvae. In one experiment the larvae were kept in complete darkness between tests. Food was not given between tests except, in some cases, towards the end of the experiment.

The results of these experiments (figs. 2 & 3) showed that, over a period of about a week after extraction from mud, there was a steep rise in the proportion of

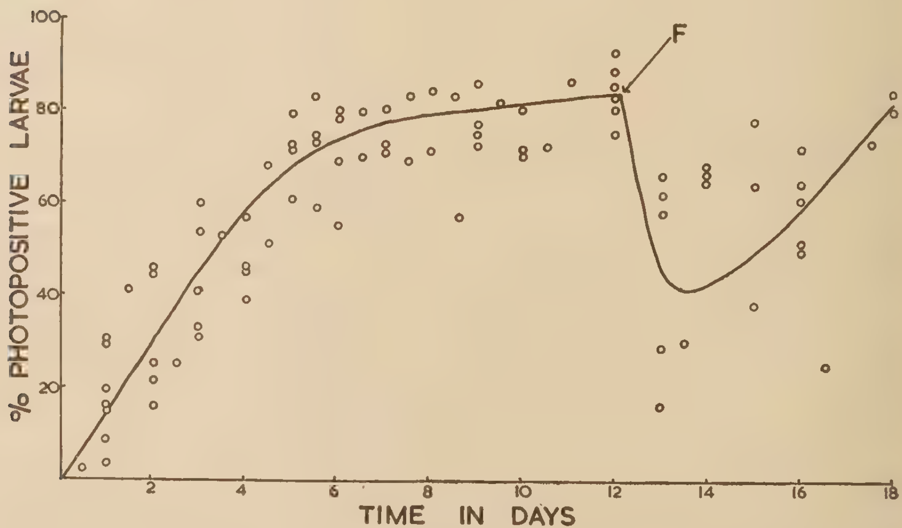


Fig. 2.—The typical reaction to light of groups of unfed fourth-instar larvae of *C. circumscriptus* over a period of time after extraction from mud, showing the change which occurs on feeding with blowfly larvae (F).

positively phototactic larvae. Thereafter, in the case of fourth-instar larvae, the curve began to level off between 70 and 90 per cent., while that of the third instar reached 100 per cent. The larvae kept in darkness between tests showed no difference in behaviour.

In six of the experiments, larvae of the fourth instar, after having been tested without food over periods of about 12 days, were fed with stained blowfly larvae, which were renewed daily along with the water in the dishes. After one day's

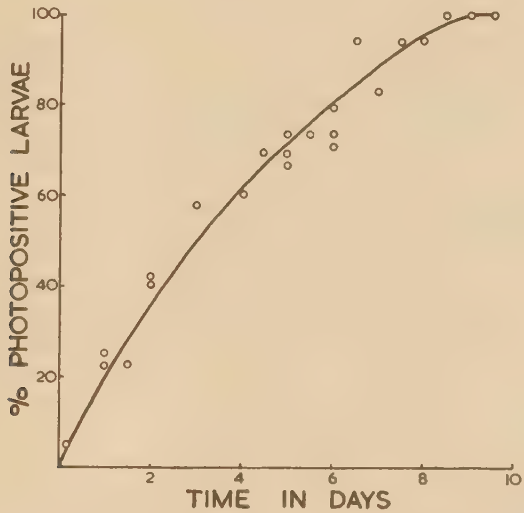


Fig. 3.—The typical reaction to light of groups of unfed third-instar larvae of *C. circumscriptus* over a period of time after extraction from mud.

feeding the proportion of photopositive larvae dropped on the average from 83 to 40 per cent., after which, in spite of fresh supplies of food, it began to rise again. A considerable variation in the degree of reversion to photonegative taxis is undergone by different groups (fig. 2). Nevertheless, this temporary reversion was quite marked in all cases.

From all six experiments, an average of 70 per cent. of photonegative larvae and 64·0 per cent. of photopositive larvae had visible food in the alimentary canal. Since without doubt some of the larvae fed on unstained tissues these figures may represent a slightly low estimate of the actual number of fed larvae.

In a further set of experiments, fourth-instar larvae were kept in dishes of water for about a week, after which time they were tested. Those which had developed a photopositive reaction were separated from the rest. Two batches of the photopositive larvae were put into dishes containing culture medium and a further two batches were put into mud which had been previously dried, powdered, incinerated, and reconstituted with water, thus destroying all organic matter, while the pH was unchanged. Since this incinerated mud did not have the same flocculence as the culture medium, some of it was mixed with enough " Dyox " powder (probably methyl cellulose) to give it an approximately similar texture. Some Trypan Red stain was added to this mixture, and a fifth batch of larvae was then placed in it.

The larvae were recovered at intervals by flotation in magnesium sulphate, tested for phototaxis, and returned to fresh medium.

The results of these tests show that, in the case of larvae placed in culture medium, the proportion of photopositive individuals dropped quickly to between 20 and 30 per cent., where it remained as long as the experiment lasted (fig. 4, broken line). The proportion of photopositive larvae with material in the alimentary canal was 38·4 per cent., while that of the photonegative larvae was 74·6 per cent. In the experiments in which the larvae were kept in incinerated mud, the proportion of photopositive larvae remained at or very near 100 per cent. (fig. 4, solid line). This was also the case where "Dyox" was mixed with the medium (fig. 4, dotted line). Of the larvae kept in incinerated mud very few had

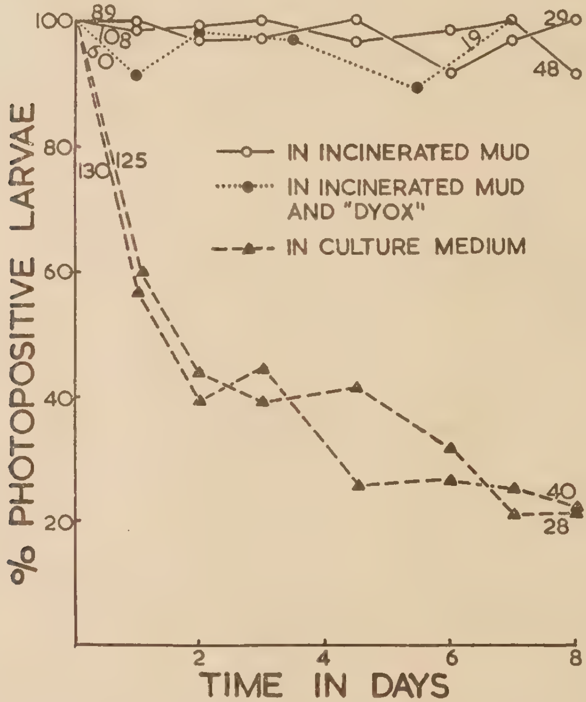


Fig. 4.—The reactions to light of groups of previously starved fourth-instar larvae of *C. circumscriptus* after placing in different media. The numbers of larvae at the beginning and end of each experiment are shown.

any material in the alimentary canal. Of those kept in the mud-"Dyox" mixture, all had material in the gut a few days after the beginning of the experiment. When a number of these were dissected this material proved to be almost exclusively "Dyox".

Tests carried out immediately after recovery from mud on larvae which were in the latter stages of the fourth instar showed that the proportion of photopositive individuals rose somewhat more steeply (fig. 5) than was the case for younger larvae of the same instar (*cf.* fig. 2). Further, the curve does not flatten out but continues until all are photopositive. During these experiments large numbers of pupations took place.

Similar tests were carried out on batches of unfed fourth-instar larvae of *C. maritimus* Kieff., a species found in the same habitat as *C. circumscriptus*.

These showed marked differences in behaviour towards light (fig. 6). At first there was a rise in the proportion of photopositive larvae, but this was much more gradual than in the case of *C. circumscriptus* (*cf.* fig. 2) and did not reach the same high figure. Afterwards the proportions fluctuated to such an extent that when food was provided the drop in the curve could not be considered significant.

(*b*) *Conclusions and discussion.*—When the larvae of *C. circumscriptus* are extracted from the mud of their habitat the majority are negatively phototactic.

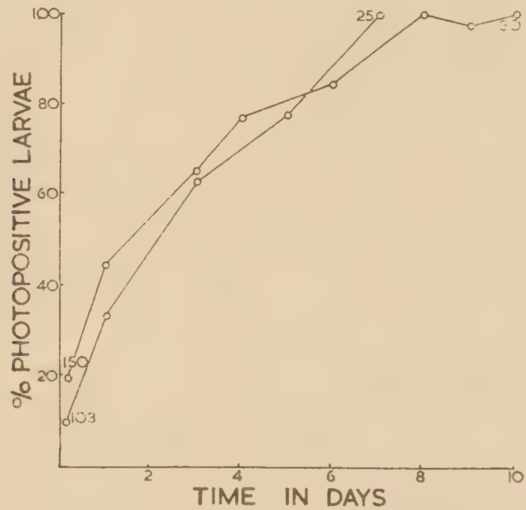


Fig. 5.—The reactions to light of two groups of unfed late fourth-instar larvae of *C. circumscriptus* over a period of time after extraction from mud. The numbers at the beginning and end of each experiment are shown.

However, when they are kept in fresh water over a period of time, without food of any sort, an increasing proportion of them become positively phototactic, this proportion levelling off after about a week and remaining fairly constant somewhere between 70 and 90 per cent. of the total number. There is no difference in this pattern when the larvae are kept in darkness between tests, so that it is unlikely that the change in taxis of larvae exposed to light between tests can be explained as facilitation to light conditions. This is confirmed by the fact that reversion to photonegative behaviour can be brought about by feeding, although the larvae are kept in the light.

When food is given to the larvae there is a rapid drop in the percentage of photopositive individuals. If the food consists of chopped-up blowfly larvae, this low proportion is not maintained but sooner or later begins to rise again, in spite of fresh supplies of food being given, until once more it reaches the level which existed prior to feeding. If, however, the larvae are kept in culture medium between tests, the percentage of photopositive larvae continues to fall until a level of between 20 and 30 per cent. is reached and maintained. In contrast, if larvae which have become photopositive are kept in mud containing no nutritive organic matter this does not occur.

It is apparent from the results of these experiments that the behaviour of the larvae of *C. circumscriptus* is profoundly affected by hunger. Fully fed larvae exhibit a negative phototaxis but hungry larvae are positively phototactic. This is further borne out by the relative numbers of fed and unfed larvae in both

photopositive and photonegative groups. In the experiments involving the use of culture medium, the average proportion of the photopositive larvae whose alimentary canals contained material at the time of testing (38·4%) was much lower than in the case of the photonegative larvae of which 74·6 per cent. showed evidence of having fed. When the food consisted of blowfly larvae the difference was not nearly so clear-cut (64·0 and 70·7%, respectively) and it must be concluded from this, and also from the fact that reversion to photonegative taxis

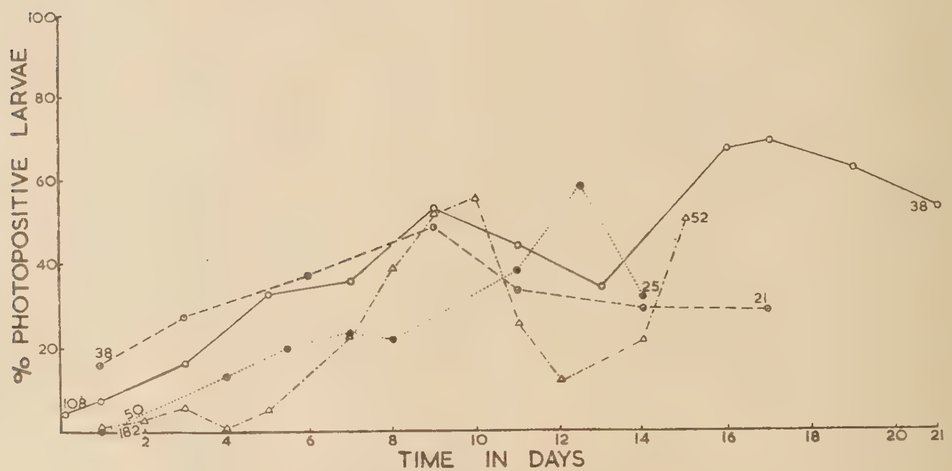


Fig. 6.—The reactions to light of four groups of unfed fourth-instar larvae of *C. maritimus*, over a period of time after extraction from mud. The numbers at the beginning and end of each experiment are shown.

was only temporary, that this food was inadequate or at the most only temporarily adequate for the nutritional requirements of the majority of the larvae.

It will be noted from these figures that, after feeding, a considerable proportion of the larvae which had material in the gut still remained photopositive and, conversely, many of the apparently unfed larvae were photonegative. This is no doubt partly due to experimental error, but apart from this a number of reasons may be suggested to explain this apparent anomaly. In the first place, the material ingested by these photopositive larvae may not have been digested at the time of testing, or may not have contained enough nutritive matter to effect a reversion to photonegative behaviour, or may not have been of the type required for this to be achieved. Secondly, the photonegative larvae which were apparently unfed may, in fact, have ingested colourless food, or may have defaecated all waste material from a previous meal and were not yet hungry enough to show photopositive reactions.

The negative phototaxis of the well-fed larvae, and its reversal to a positive phototaxis when starved, has a biological significance under natural conditions. Loeb (1889) has shown that the young caterpillars of the moth, *Euproctis similis* (Fuessly) (cited as *Porthesia chrysorrhoea* (L.)), exhibit a positive phototaxis before feeding, which is lost after they have fed. The larvae under natural conditions are directed by this initial taxis to the leaves at the top of the branches where they find their food. Brandt (1937) demonstrated a similar phenomenon with the caterpillars of *Lymantria monacha* (L.). Neither of these cases illustrates the complete and immediate change of taxis on feeding which has been shown to occur in *C. circumscriptus* and one must turn to the Platyhelminthes for a

more analogous record. Beauchamp (1933) has shown that when *Planaria alpina* is developing sexually it is positively rheotactic and becomes negatively rheotactic on completing the sexual cycle. This change from positive to negative rheotaxis may also be brought about by starvation and if the starved animals find food they again become positively rheotactic.

The ecological significance of the behaviour of *C. circumscriptus* towards light can be appreciated by studying their feeding habits. Observation has shown that a large part of the larval life is spent burrowing below the surface of the mud where protection and some food may be had. It has been shown by Megahed (*op. cit.*) (in *C. nubeculosus* (Mg.)), and confirmed in the present work with *C. circumscriptus*, that feeding also occurs on the surface. Thus it would appear that, while the larvae are generally photophobic and spend most of their time under the surface, the need to feed at the surface brings about a reversal of this reaction. When the larvae are fully fed they again become negatively phototactic and retreat to safety below the mud. It is apparent that this behaviour may be used to determine the food requirements of the larvae, and a second series of experiments, designed to do this, is described below.

When photopositive larvae were kept in the mixture of incinerated mud and "Dyox" it was found that eventually all of them ingested "Dyox" but, nevertheless, did not exhibit the reversion from positive to negative phototaxis typical of fed larvae. It is evident from this that the mechanism controlling their reactions to light is not influenced by the mere presence or absence of material in the alimentary tract, but that reversion from photopositive to photonegative behaviour will only take place if the material ingested can be utilised as food by the larvae. Conversely, it may be assumed that the reversal from photonegative to photopositive behaviour is initiated not by an empty gut but by what may be called "physiological" hunger.

It is not fully understood why, under starved conditions, the proportion of photopositive larvae usually becomes stable between 70 and 90 per cent. and rarely approaches 100 per cent. At present it can only be supposed that a small number of larvae may obtain food by eating their dead or dying companions, which they have frequently been seen to do. The latter were removed at each test but, since mortality occurred continually and increased with time as the experiment progressed, some food of this nature was always available.

When larvae in the latter stages of the fourth instar were tested (fig. 5), the proportion of photopositive individuals rose somewhat more steeply than in younger larvae of the same instar and all eventually became photopositive. Pupation occurred constantly throughout the experiments. In these cases it must be assumed that, as well as hunger, another factor is also helping to bring about the change from negative to positive phototaxis. It has been observed that before the larvae pupate they come to the surface of the mud and lie in regions covered only by a thin film of water. It would appear that this is achieved by a reversal from photonegative to photopositive taxis probably initiated by the physiological changes connected with pupation. Because of the rapid reductions in the numbers due to pupation it was not possible to make reliable tests on the effect of feeding.

When third-instar larvae were tested, they too all became positively phototactic but, because of the small numbers (see p. 788) available at the time of the experiment no reliable conclusions may be drawn from the data obtained. During the experiment, however, their numbers were further reduced by many moulting to become fourth-instar larvae and the possibility should not be overlooked of a temporary reversal to a photopositive taxis, associated with impending ecdysis, that may take place, thus increasing the percentage of photopositive larvae. An investigation of this point may well prove worthwhile.

Considering the conditions under which the larvae of *C. circumscriptus* live in

the field it must be assumed that, since the light could not penetrate more than a small fraction of an inch below the surface of the mud, their behaviour towards light stimuli can be nothing more than a maintenance reaction with the function of keeping them at the surface until they have obtained adequate nourishment, and driving them below afterwards. Some other tropism must operate to bring hungry larvae, below the surface, within reach of the light and, perhaps, to keep fully fed larvae below the surface. While no attempt has been made to investigate this point, it has been noted during the experiments that the photopositive larvae not only swam towards the light but many of them also were found swimming upwards towards the surface of the water at the illuminated end of the trough. It may be that the larvae can appreciate changes in pressure in the tracheae so that, when it is necessary for them to feed on the surface, they move upwards to levels where that pressure is at a minimum. Alternatively, the reaction which brings them to the surface may be simply a negative geotaxis, though it is not known whether the larvae possess any sense organs which might receive gravitational stimuli. Brandt (*op. cit.*) has shown that the young unfed larvae of *Lymantria monacha* are negatively geotactic as well as positively phototactic. It is probable that the behaviour of the larvae of *C. circumscriptus* in relation to feeding is the result of a similar combination of reactions.

Finally, the differences in behaviour between *C. circumscriptus* and *C. maritimus* are worthy of mention. In tests made 24 hours after extraction from the mud, an average of only 6·0 per cent. of the larvae of the latter species were photopositive compared with an average of 17·7 per cent. in the case of *C. circumscriptus*. The increase in the number of photopositive larvae is much slower and lasts longer, after which the curve begins to fluctuate. Also, the proportion of photopositive larvae seldom becomes as large as that found in *C. circumscriptus*. This difference in behaviour may be correlated with feeding habits. The larvae of *C. maritimus* are much more plentiful in places where there are reeds whose roots make the ground much firmer than on the sites favoured by *C. circumscriptus*. They show, moreover, a greater tendency to burrow more deeply into the mud, an average of only 51·2 per cent. occurring in the top inch as compared with 78·5 per cent. in the case of *C. circumscriptus*. It may be the case, therefore, that under natural conditions a larger proportion of their food is found below the surface of the mud, and thus their reactions to light stimuli are not so well marked and consistent.

It is likely, therefore, that other species of *Culicoides* may show different patterns of behaviour towards light, according to their habits in the field, and the use of this phenomenon as a tool to determine their food requirements is thus limited.

Second series.

(*a*) *Details and results.*—In the light of the foregoing results and conclusions, a further series of phototactic experiments was conducted in an attempt to establish the types of food taken by the larvae. In each of these a number of larvae, which had been previously starved and found to be positively phototactic, were placed in various media and tested at intervals for response to light, and were also examined for the presence of material in the alimentary canal. Results are shown in figs. 7–9 and Table I.

In the first experiment, the larvae were kept in mud which had been newly reconstituted from dried powdered mud of the type used for making culture medium. During the tests most of the larvae maintained their photopositive behaviour (fig. 7, dotted line). Very few showed any indications of having fed (Table I).

Secondly, larvae were kept in the supernatant fluid which was decanted from " matured " culture medium. Tests showed (fig. 7, broken line) that there was

initially a gradual drop in the proportion of photopositive larvae to 51·5 per cent., but this was not maintained, and at the end of the experiment this figure had risen again to 73·3 per cent. Examination of the larvae showed, rather surprisingly, that a larger percentage of the photopositive larvae had material in the alimentary canal than was the case among the photonegative larvae.

TABLE I.

The percentages of larvae of *C. circumscriptus* which had visible material in the alimentary canal after being kept in various media between tests for reactions to light.

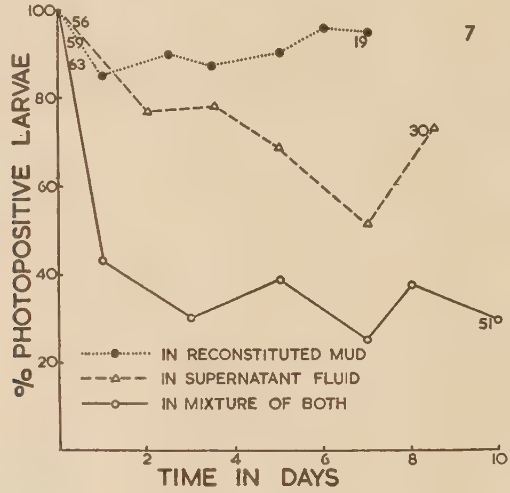
Medium	Photopositive larvae	Photonegative larvae
Water with stained blowfly larvae	64·0	70·7
Culture medium	38·4	74·6
Incinerated mud	4·3	6·3*
Incinerated mud and "Dyox"	88·0†	83·0†
Newly reconstituted mud	0·6	4·2*
Newly reconstituted mud and supernatant liquid from culture pots	49·8	88·3
Supernatant liquid from culture pots	60·7	47·2
Surface of culture medium	71·8	72·2
Sub-surface culture medium	63·4	77·5

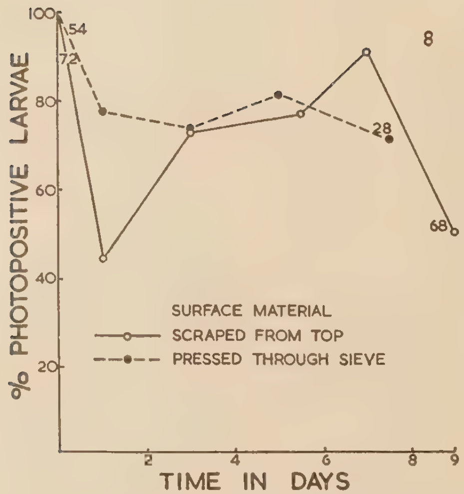
* Figures unduly high due to the small number of larvae which became negatively phototactic in these experiments.
† In the latter part of this experiment all the larvae in both groups had material (almost exclusively "Dyox") in the gut.

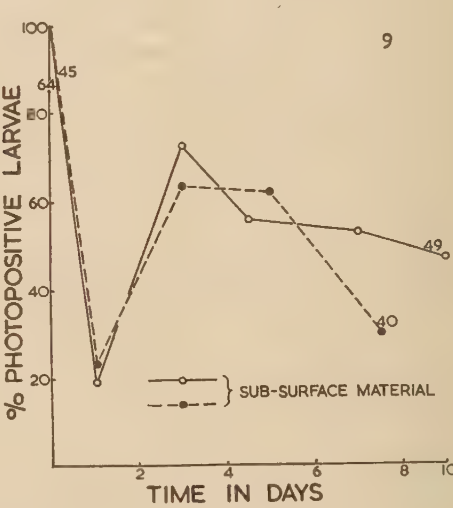
In the third experiment, powdered mud was reconstituted with the supernatant fluid. Kept in this medium, the proportion of positively phototactic larvae fell quickly (fig. 7, solid line) and fluctuated throughout the experiment between about 25 and 40 per cent. There was a considerable difference in the proportions of photopositive and photonegative larvae that had material in the alimentary canal.

In a further two experiments, the larvae were given the opportunity to feed on material on the surface of the culture medium. In one, the material was carefully scraped off the surface of the medium and mixed with a little of the supernatant fluid, and in the other, the larvae were placed in a small sieve of 80-mesh wire gauze which was pressed on to the surface of the culture medium, so that they were able to feed directly on the surface material that was squeezed through the mesh. Light tests showed that in the first case, though the percentage of photopositive larvae dropped initially (fig. 8, solid line) it rose subsequently and then dropped again. In the second case the drop was not so great and the proportion of photopositive larvae maintained itself between about 70 and 80 per cent. (fig. 8, broken line). There was little difference in either experiment in the percentage of photopositive and photonegative larvae with material in the alimentary canal, this being high in both cases (figures combined in Table I).

In the last two experiments the larvae were placed in mud taken from the bottom of the culture pots and mixed with tap water. In each, the percentage of photopositive larvae dropped quickly only to rise and fall again (fig. 9). There was an appreciable difference in the percentage of larvae of the two groups which had material in the alimentary canals but these percentages were nevertheless high in both photopositive and photonegative groups.







Figs. 7–9.—The reactions to light of groups of previously starved fourth-instar larvae of *C. circumscriptus* after placing in different media. The numbers at the beginning and end of each experiment are shown.

(*b*) *Conclusions and discussion.*—Of both first and second series of experiments, only in those where the food offered was culture medium or powdered mud reconstituted with the supernatant fluid from "mature" culture pots did the majority of the larvae revert to a photonegative taxis which was maintained throughout the experiment. From this and the fact that there was a considerable

difference in proportions of photopositive and photonegative larvae with material in the gut (Table I), it may be assumed that these are the most adequate of the media which have been tested.

The larvae would not feed on newly reconstituted mud. It would thus appear that the ingredients on which they feed are present (or become edible) only after the period of maturation to which the culture pots were subjected. When the mud powder was reconstituted with the supernatant fluid from culture pots, feeding and reversion of taxis took place. This would indicate that the food ingredients necessary for this to occur are present in the supernatant fluid, yet when photopositive larvae were put into this alone, only 50 per cent. of the larvae, at the most, became photonegative, and only temporarily at that.

From the result of this last experiment it was thought that the food sought by the photopositive larvae might lie on the immediate surface of the mud rather than in the supernatant fluid. At attempt to demonstrate this was made in the experiments using material from the surface, but here again, the majority of the larvae failed to show a permanent reversion to photonegative behaviour.

Paradoxically, when larvae were offered mud taken from the bottom of the culture pots, there was an immediate drop in the proportion of photopositive larvae after which fluctuations occurred. Since some of the material ingested consisted of green algae, it must be assumed that the medium, while being taken from the culture pots, became contaminated with material which had probably oozed from the surface beforehand, so that it retained in part at least, the characteristics of " whole " culture medium.

Megahed (*op. cit.*) has described the feeding of *C. nubeculosus* as seen on the surface, and the behaviour of *C. circumscriptus* agrees in general with his description. He also states that the feeding of the larvae is concentrated on the surface or the top few millimetres of the mud. There seems little doubt, however, that a considerable amount of feeding also takes place below these levels. It has been shown by Kettle & Lawson (*op. cit.*) and confirmed by the author's own observation, that a substantial proportion of *Culicoides* larvae are found well below the surface of the mud. Observations on the larvae of *C. circumscriptus* in culture pots indicate that at any given time only a small fraction of the total number of larvae in the pots occurs on or just under the surface. Since the larval stage in insects is generally that in which feeding is almost constantly taking place it is reasonable to suppose that the midge larvae also do so while below the surface of the mud. Larvae which have been newly recovered from marshes often have brown material in the alimentary canal and, while some of this may have been ingested on the surface, it is significant that those larvae which were kept in mud taken from the bottom of culture pots ingested more of this brown material than those kept in material taken from the surface only.

It has been suggested in the discussion of the first series of experiments that the positive phototaxis which occur in starving larvae enables the larvae in nature to supplement its diet with material found on the surface of the mud. Under natural conditions such larvae would have already fed on sub-surface material and after satisfying their requirements would again revert to photonegative behaviour and descend below the surface of the substrate. Why then, do the larvae, having been given material taken from the surface, not show this change in taxis as clearly as those which were kept in complete culture medium?

It is suggested that the reason for this unexpected behaviour lies in the fact that the larvae used in the laboratory experiments had been starved completely and had no food at all in the alimentary canal. Such a contingency would not arise under natural conditions where they would have had available plenty of sub-surface food before becoming positively phototactic and would have reverted to negative phototaxis before this was expended.

It would seem, therefore, that the need for surface food which brings about the positive phototaxis continues to operate because the larvae are also starved of sub-surface food. Although it would seem logical that such a need would be satisfied by a photonegative taxis this does not in fact occur since the circumstances do not apply in their natural habitat. Starvation of any kind, therefore, would bring about a positive phototaxis.

General Observations and Discussion on Feeding.

The experiments described above give us no information regarding the exact constituents of the diet taken by the larvae of *C. circumscriptus* and it is likely that these are of a varied nature. However, they do indicate that food of two different types is required and that these are obtained from two distinct sources. The larvae spend the greater part of their time feeding below the surface but at intervals they come to the surface, having reversed their normal photonegative taxis. Having obtained the surface food they require they revert to a photonegative taxis and return to continue feeding below the surface.

When the larvae are examined immediately after recovery from mud, the alimentary canal is seen to contain material which varies in colour from cream to dark brown. The alimentary canals of many specimens were dissected out and squashed on a slide, but in no case was it possible to recognise with any degree of certainty the material they contained.

It has been assumed that the darkly coloured contents consisted of mud or the organic débris present in the habitat, and this is borne out by the investigations of Mayer (1934*a*) who has shown that coarse detritus and diatoms comprise the main bulk of the food of one group of midge larvae.

When the larvae are kept in water which contains green algae the appearance of green matter in the gut shows that these are ingested. This is also seen in larvae reared in culture medium which has a growth of algae, and is in this case mixed with brown material. Algae are reported as a constituent of the food of various species by Bequaert (1925), Painter (1927), Leathers (1923),* Lang (1931), Mayer (1934*a*), and Séguy (1950). However, when the larvae of *C. circumscriptus* feed on green algae, faeces of this colour may be seen in the rectum, as has been reported in *C. nubeculosus* by Megahed (*op. cit.*) who concludes that some at least must be indigestible and is not used by the larvae. This view is supported by the facts that *C. circumscriptus* does not thrive in a culture containing mostly green algae and that both this species and *C. nubeculosus* can develop normally in culture medium containing no algae.

It is also noteworthy that when starving larvae of *C. circumscriptus* were placed in the supernatant fluid of culture pots, which was rich in green algae and flagellates, it was in the photopositive groups that a greater percentage of larvae had ingested green material. As a rule, in the feeding experiments, the greater percentage of larvae which had swallowed material was found in the groups which had become photonegative (see Table I). This unusual result also indicates that algae are at least not an important part of the diet.

Carnivorous feeding by *Culicoides* larvae has been reported by Pratt (1907), who stated that the larval food of *Culicoides guttipennis* (Coq.) (cited as *Ceratopogon*) appeared to be the débris at the bottom of the water-filled tree holes in which the larvae were found, as well as dead mosquito and other larvae, and cast larval and pupal skins. The larvae were seen to feed on a larva of a species related to *Eristalis* and of a Dascillid beetle. Lutz (1912) states that some species feed on the decaying food of crabs. Thomsen (1937) and Hill (1947) are of the opinion that the larvae are cannibalistic.

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* Leathers' identification of the larvae he studied is disputed by Mayer (1934*a*) who identifies them not as *Culicoides* sp. but as *Dasyhelea* sp.

Carnivorous feeding has also been observed in *C. circumscriptus.* For experimental purposes the larvae were kept for a varying number of days in dishes of newly reconstituted mud together with larvae of other types. On recovery many of the latter were found to be dead or missing altogether. Empty cuticles of the latter were recovered which were being gnawed by midge larvae. Dead Ephydrid and Limnobiid larvae were found with small holes in the body wall and in some cases midge larvae were seen with their heads thrust into the holes, vigorously attacking the internal tissues. In others, the midge larvae had wholly entered the bodies of the larger larvae and could be clearly seen feeding on the tissues. Midge larvae have also been observed feeding on the dead remains of their companions and also on the pupae. They frequently attack and devour newly formed pupae.

Some doubt exists as to whether the larvae of *Culicoides* and other members of the CERATOPOGONIDAE are true predators. Many writers are of the opinion that they are detritus feeders which attack only dead or moribund insects, but Weerekoon (1953) has observed an undoubted case of true predation in the larvae of *Bezzia* sp. which he saw attacking and feeding on the larvae of *Palpomyia quadrispinosa* Goetgh. He is also of the opinion that animal matter plays a much more important rôle in the feeding of Ceratopogonid larvae than has generally been realised. The truth of this assumption is not borne out in the case of *C. circumscriptus*. The larvae do not appear to be true predators. Apart from the vulnerable and helpless new pupae, no instance has been observed of midge larvae attacking and killing healthy insects. On many occasions they have been seen to nibble at their companions for a few moments with their mandibles but no case of penetration or killing has been observed. From the results of the experiments on phototaxis made on larvae fed on insect flesh there is also reason to suppose that it does not constitute an adequate diet.

Observations also indicate that they will eat insect flesh only when no other food is available. When pieces of blowfly larvae were added to cultures of midge larvae containing plenty of other organic matter they eventually putrefied without apparently being eaten. In the field, the larvae may occasionally feed on the bodies of their own and other species but this would not appear to be a major constituent of their diet, for when gauze bags containing pieces of blowfly larvae were laid in the mud of their natural habitat as traps and left for periods of up to a week they were found on recovery to contain only one or two *Culicoides* larvae, if any at all.

The larvae appear to be primarily detritus feeders, feeding mainly on vegetable matter, both living and non-living. Although some of the green material from ingested algae and flagellates is voided in the faeces it is unlikely that they are completely devoid of food value since the alimentary canal is often full of them to the exclusion of other materials. Leathers (*op. cit.*) and Lang (*op. cit.*) state that *Culicoides* larvae also feed on bacteria and this has been confirmed with *C. nubeculosus* by Megahed (*op. cit.*) and by the author's observations on *C. circumscriptus*.

The question has arisen as to whether the larvae are selective or not in their feeding. Megahed states that in culture pots *C. nubeculosus* feeds with little discrimination on the available organic matter. Lang states that *Culicoides* larvae do not swallow mud and will grow and metamorphose in an aquarium lacking plants and animals, apparently living on bacteria and nannophytoplankton. He concludes from this that they are selective filter feeders. Mayer (1934*a*) was able to identify, among other things, detritus and sand in the gut contents. He rejects Lang's hypothesis of selection and accounts for the differences in the constituents and particle size of the food in two groups of species by the variation in size and sucking strength of the pharyngeal skeleton.

The larvae of *C. circumscriptus* are certainly selective in their feeding. On

the surface of culture pots their feeding activity appears to be very discriminatory. They nibble in one spot, leave it and go elsewhere, constantly changing their position as if searching for particular types of food. In spite of this however, I feel that Lang's hypothesis of selection is based on false premises. The presence of detritus and comparatively large particles of material in the alimentary canal shows that the larvae do not confine their feeding to finely divided material. When the larvae of *C. circumscriptus* are kept in a medium similar to that described by Lang, their rate of development is slowed down. Unless the species (unnamed) on which Lang based his conclusion has a diet radically different from that of other species it must be supposed that they were already well-advanced in maturity at the time of his observation.

Mayer's hypothesis of non-selective feeding, as applied to *Culicoides* larvae, is likewise contradicted by observation and experiment. The indiscriminate ingestion of the substrate which he reports in *Bezzia* (Mayer, 1934*b*) does not occur in *C. circumscriptus*. It has been shown (Table I) that if the larvae are kept for as long as a week in mud containing no organic matter or in mud which has been freshly reconstituted from powder, hardly any of them ingest it.

It seems probable that at least three factors are involved in the choice of food. Firstly, the darting searching movement of the larvae on the surface of the culture pots indicate that the surrounding material is being tested for sapidity and that the most acceptable constituents are ingested. That chemoreception plays a part in food choice is also borne out by the fact that some substances such as insect flesh are not eaten when other food is available.

Secondly, the texture of the prospective food material seems to influence its selection. The larvae not only refuse to ingest incinerated mud—which is probably equally non-attractive to their chemoreceptors—but neither will they take any of the material available in newly reconstituted mud which contains plenty of organic matter. This would also explain why "Dyox" was ingested when mixed with incinerated mud. It was probably acceptable to their "texture receptors" although their chemoreceptors would not register it as a sapid material.

The sensillae which control the choice of food are not known. It may be safely assumed that they are situated on the head. Lawson (1951) and Kettle & Lawson (*op. cit.*) have reported the presence of various sensillae on the labrum of *C. nubeculosus* and other species, but as yet we have no information regarding their function.

Lastly, as suggested by Mayer (1934*a*), there is reason to suppose that there is some mechanical selection with regard to particle size of the ingested material, carried out by the pharyngeal skeleton, in particular by the teeth borne on the epipharynx.

It is, of course, inevitable that particles of sand and mud would be ingested along with the food, hence Mayer's discovery of these materials in the larval gut. It is contended, however, that this does not indicate non-selective feeding but that the ingestion of non-nutritive materials is accidental and incidental to the ingestion of food, and that it is not ingested merely that food may be extracted from it.

Summary.

The larvae of *Culicoides circumscriptus* Kieff. are mostly negatively phototactic when extracted from mud and placed in water. Experiments show, however, that if kept without food over a period of time a large proportion becomes positively phototactic. The provision of food causes them to revert to a photonegative taxis which may be permanent as long as suitable food is given, or temporary if the food does not satisfy their nutritional requirements. On the

other hand, the provision of a completely non-nutritive medium does not bring about such a reversion. The significance of this behaviour is discussed in the light of the habits of the larvae in the field.

Most of the experiments were carried out with batches of fourth-instar larvae, but in a few, third-instar larvae and fourth-instar larvae near to pupation were used. From the results it is suggested that the processes of ecdysis and pupation may bring about a reversal from photonegative to photopositive taxis independent of the need for food.

The significance of the behaviour of the larvae towards light stimuli is discussed in relation to their habits in the field. It is assumed that its function is to maintain the larvae on the surface of the mud while feeding and to drive them below when they have fed, and that some other type of tropism must initially drive them to the surface or keep them below according to their nutritional needs.

It is shown that the behaviour towards light stimuli of the larvae of *C. maritimus* Kieff. differs somewhat from that of *C. circumscriptus* and reasons are suggested for this.

A second series of experiments designed to throw some light on the food requirements of the larvae is described. In a discussion on the results of these it is shown that the larvae feed on material both on the surface of the mud and below the surface, and it is suggested that larvae which have fed on sub-surface food become positively phototactic when they require food from the surface and, having fed there, revert to photonegative behaviour. If, however, photopositive larvae have not previously had the opportunity to feed on sub-surface material they continue to act as completely starved larvae and remain photopositive in spite of their having fed on surface material.

The detailed constituents of the larval diet have not been worked out. The larvae appear to be detritus feeders, feeding mainly on vegetable matter and bacteria obtained on or below the surface of the mud, though green algae are not an important part of their diet. They are carnivorous on occasion but are normally not so when other food is readily available. They are selective in their choice of food and at least three factors, sapidity, texture and the size of particles, appear to influence this selection.

Acknowledgements.

I wish to record my thanks to Professor C. M. Yonge, C.B.E., F.R.S., for the provision of facilities to carry out this work in the Zoology Department of the University of Glasgow, and to Dr. J. W. H. Lawson for his invaluable advice and criticism and for reading the manuscript.

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